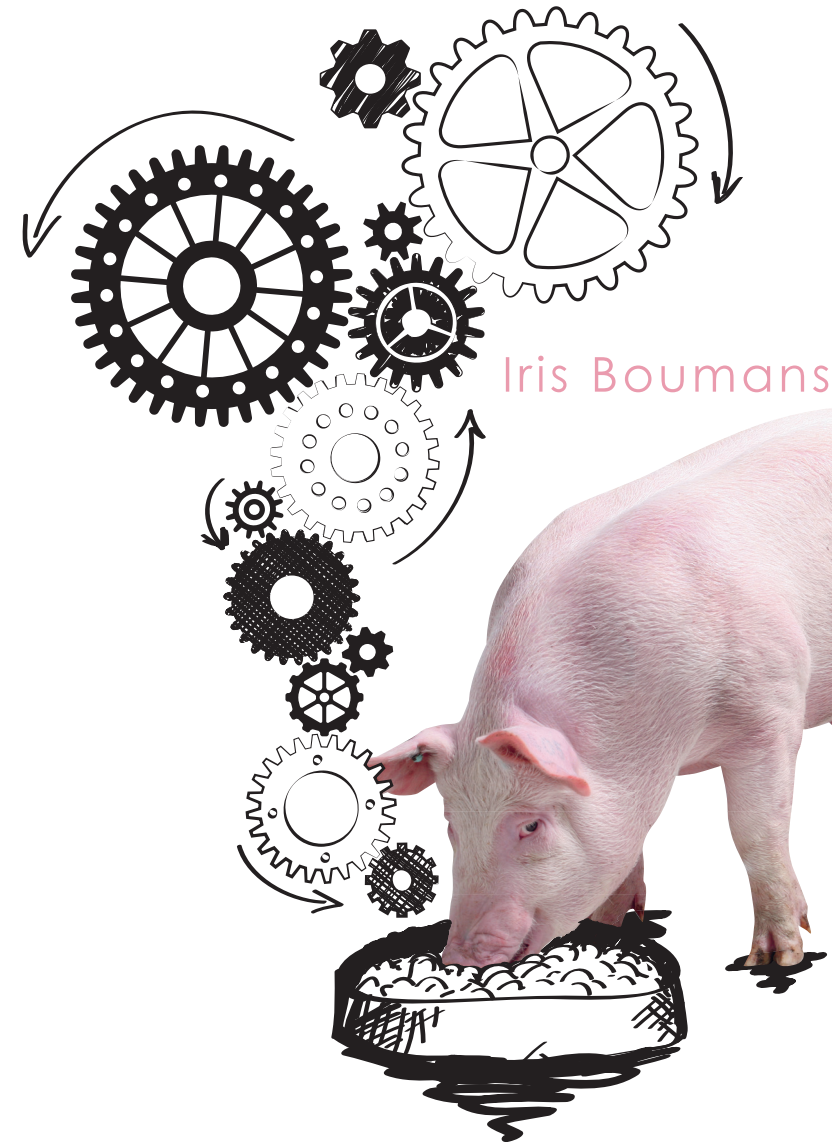
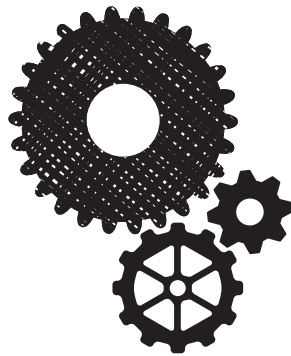


# SIMULATING PIGS

Understanding their motivations,  
behaviour, welfare and productivity



Iris Boumans

## Propositions

1. Understanding pig behaviour is essential in gaining insight into the trade-offs and synergies between sustainability issues in pig production systems.  
(this thesis)
2. Agent-based modelling increases our understanding of behaviour in a way that cannot be done empirically.  
(this thesis)
3. Despite its controversial image for human health, coffee consumption has more benefits than risks.
4. A good start for understanding why animals do what they do lies in understanding why you do what you do.
5. Rabbits have much more personality than people give them credit for.
6. Thinking of your earlier achievements is the best way to conquer any doubt about your qualities.

Propositions belonging to the thesis, entitled

‘Simulating pigs – Understanding their motivations, behaviour, welfare and productivity.’

Iris Boumans

Wageningen, 1 September 2017

# **SIMULATING PIGS**

Understanding their motivations, behaviour, welfare  
and productivity

Iris Boumans

## **Thesis committee**

### **Promotor**

Prof. Dr I.J.M. de Boer  
Professor of Animal Production Systems  
Wageningen University & Research

### **Co-promotors**

Dr E.A.M. Bokkers  
Associate professor, Animal Production Systems Group  
Wageningen University & Research

Dr G.J. Hofstede  
Associate professor, Information Technology Group  
Wageningen University & Research

### **Other members**

Prof. Dr B. Kemp, Wageningen University & Research  
Prof. Dr W.J.J. Gerrits, Wageningen University & Research  
Prof. Dr C.K. Hemelrijk, University of Groningen  
Dr M.B.M. Bracke, Wageningen University & Research

This research was conducted under the auspices of the Graduate School of  
Wageningen Institute of Animal Sciences (WIAS)

# **SIMULATING PIGS**

Understanding their motivations, behaviour, welfare  
and productivity

Iris Boumans

## **Thesis**

submitted in fulfilment of the requirements for the degree of doctor  
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# Abstract

The transition towards sustainable pig production systems is receiving increasing attention nowadays. Pig behaviour plays a central role in sustainability, as it is an important indicator for pig welfare and can also affect other sustainability issues. Understanding behaviour and related welfare consequences requires to understand motivations underlying behaviour. The two aims of this thesis were: 1) to assess the use of agent-based modelling for understanding pig behaviour and underlying motivation, and 2) to apply agent-based modelling for increasing our understanding of pig behaviour, and related animal welfare and productivity performance.

We first explored the use of agent-based modelling with tail biting behaviour in pigs as a case study. An agent-based model was developed to understand the causation of tail biting behaviour. Subsequently, we developed a mechanistic and dynamic simulation model to gain more understanding of feeding behaviour and internal (physiological) factors. The model integrates knowledge from physiology and ethology, and combines growth with a behavioural decision model based on motivation. This model included motivations underlying feeding behaviour and various feeding patterns of an individually housed growing pig. To deepen our understanding of mechanisms underlying feeding patterns of pigs within 24 hours, hormonal circadian rhythms were included in the model in a follow-up study. The circadian rhythms of cortisol and melatonin explained the alternans pattern, a small peak of feed intake at the beginning of the day and a larger peak at the end of the day, of feeding in pigs. Next, an agent-based model of feeding and social interaction in commercially group-housed pigs was developed to deepen our understanding of the complex interaction between internal physiological factors and external social factors. Social factors (e.g. competition level and social facilitation) and behavioural strategies (e.g. avoidance and approach) affected social interactions among pigs and feeding behaviour. The causation of variation among pigs was further explored in this model. Pig characteristics were important in various feeding, social interaction and growth patterns in pigs.

In general, agent-based modelling proved to be a useful method to understand animal behaviour and underlying motivations. It contributed to further understanding of tail biting, feeding and social behaviour in pigs. Furthermore, agent-based modelling showed to be a novel method to find and assess behaviours as welfare indicators, and to contribute to understanding trade-offs and synergies between sustainability issues, such as animal welfare and productivity.





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# **Chapter 1**

## **General introduction**

## **1.1 Sustainability issues in pig husbandry**

Over the last decades, pig production in developed regions has developed into specialised and large-scale production systems in adaptation to the worldwide increasing demand for pork (Steinfeld et al., 2006). More traditional small-scale farms with an outdoor run have been replaced by large-scale farms, where pigs are kept inside on concrete floors and at high stocking densities (Miele et al., 2013; Stern et al., 2005; Velarde et al., 2015). An average conventional pork production system in the Netherlands, for example, consisted of 3400 pigs and 15 ha agricultural land in 2015 (CBS, 2016). Although these systems aim to optimise production efficiency and allow maximising meat production and consumption, they are also associated with several sustainability concerns (Schodl et al., 2017; Willems et al., 2016). These concerns include environmental concerns, such as emissions that contribute to climate change, acidification and eutrophication (Dourmad et al., 2014), societal concerns, such as animal welfare and food safety (Kanis et al., 2003), and economic concerns such as farm profitability and transferability to a future generation (Ilari-Antoine et al., 2014). The transition towards sustainable pork production systems (i.e. systems being 'economically viable, ecologically sound and socially acceptable, both now and in the future'), therefore, is receiving increasing attention (Dolman et al., 2012).

In research, solutions that address sustainability concerns are often studied in isolation, for example, addressing only the environmental impact (e.g. Basset-Mens & van der Werf, 2005; Mackenzie et al., 2016). Furthermore, studies in sustainable pig farming show a large variation in addressed topics, in which especially environmental issues are well-presented, and societal and economic issues receive less attention (Schodl et al., 2017). Sustainability, however, is a multidimensional concept in which economy depends on society and they both depend on environment (Giddings et al., 2002). Consequently, sustainability concerns should be addressed holistically with a systems approach, which can improve our knowledge to develop sustainable pig production systems (Schodl et al., 2017).

### **1.1.1 The role of animal welfare in sustainability**

Animal welfare is the most emphasised societal issue in pig farming research (Schodl et al., 2017) and plays an important role in sustainable pig production (Chemineau, 2016; Dawkins, 2017; Keeling, 2005). Concerns about animal welfare increased simultaneously with the development of current modern pig production systems (Tucker et al., 2013). Although consumers find animal welfare important, they generally rank other societal issues, such as reducing poverty, higher than animal welfare and might have a different understanding of animal welfare than experts (Lassen et al., 2006; Thorslund et al., 2017). Public concern about animal welfare can affect policy and regulation, which can lead to a ban on certain housing systems and

management practices, such as the ban on battery cages for laying hens (see review Tucker et al., 2013). In pigs, concerns about animal welfare have resulted in a European declaration to end surgical castration in pigs voluntarily in 2018 (Borrisser-Pairó et al., 2016) and some national initiatives to reduce or support a voluntary ban of tail docking in pigs in the near future (Spoolder et al., 2016).

As commonly acknowledged nowadays, three approaches can be considered in evaluating animal welfare: basic health and functioning, natural living and affective states (Fraser, 2008). As explained by Fraser (2008), basic health and functioning includes aspects such as health, growth, and ability to maintain homeostasis; natural living includes the ability to express normal behaviour, such as foraging and exploration behaviour in pigs; and affective states include feelings and emotions, such as hunger and pain.

The transition towards specialised, large-scale and controlled housing systems has affected pig welfare concerning all three welfare approaches, both negatively and positively (Keeling, 2005; Tucker et al., 2013). Negative effects, for example, are practices that can cause pain and distress, such as tail docking (Sutherland et al., 2011), or the absence of substrates to perform natural behaviours, such as rooting (Van de Weerd & Day, 2009). Examples of positive effects of intensification are a better climate control system and improved veterinary control, such as vaccination schemes (Tucker et al., 2013).

Current improvements of pig welfare often focus on improving the housing system, such as providing more space or decreasing stocking density, and/or improving management practices, such as providing enrichment materials like straw (e.g. Hemsworth et al., 2013; Lyons et al., 1995; Vermeer et al., 2014). A change in a housing system or management practice, however, can simultaneously affect multiple aspects of animal welfare. Straw-bedded housing in pigs, for example, can reduce tail biting behaviour and lameness, but can also increase respiratory problems compared to fully-slatted housed pigs (Scott et al., 2006). Additionally, improvements for welfare can affect other sustainability issues. Reducing stocking density and increasing space allowance, for example, can improve productivity and welfare of pigs, but might increase housing costs per kg pork produced, and as such reduce farm profitability (Vermeer et al., 2014). In addition, improvements that affect productivity also affect the environmental footprint per kg of animal product and thus can affect environmental impact both positively and negatively (Chemineau, 2016).

### **1.1.2 Exploring trade-offs and synergies**

Due to the multiple interactions between sustainability issues in pig production systems, optimising sustainability of these systems will include trade-offs and synergies and the challenge is to find those conditions that minimise trade-offs and

maximise synergies. Developing a model that includes trade-offs and synergies would require a holistic approach that contains both positive and negative effects on sustainability performance (Chemineau, 2016). Several studies modelled trade-offs between economic and environmental indicators (e.g. Dekker et al., 2011; Dolman et al., 2012; Thomassen et al., 2009; Van Calker et al., 2004), but could not (sufficiently) incorporate animal welfare and the effect of farmers' interventions on animal welfare in their models. Some studies explored economic and environmental consequences of animal-friendly farm scenarios. These studies, however, are based on perceptions of consumers and experts (Den Ouden et al., 1997) or a description of a theoretically improved housing system for pigs (Stern et al., 2005). As a consequence, these kind of models assess animal welfare based on the environment, such as minimum space and feeding places. Although so-called resource-based measurements will give an indication for animal welfare risks or opportunities, they do not represent the actual welfare status of animals. Many factors, besides the living environment of the animals, can affect animal welfare, such as characteristics of the animal itself (e.g. age, breed, social dominance rank) and the quality of stockmanship (e.g. handling animals, management of problems) (Blokhuis et al., 2008; Keeling, 2005). Nowadays, it is generally agreed and accepted that animal-based measurements, especially measurements on animal behaviour and health, are key for assessing animal welfare (Duncan, 2005; Welfare Quality®, 2009).

### **1.2 Centrality of behaviour in sustainability**

Pig behaviour plays a central role in sustainability, as it is an important indicator for pig welfare and can also affect other sustainability issues. Behaviour is an important mechanism for animals to control and cope with their environment (Mench, 1998). For all animal welfare approaches, i.e. basic health and functioning, natural living and affective states, the animal's state can be inferred from its behaviour. Reduced feeding behaviour, for example, can indicate basic health and functioning problems (e.g. decreased feeding motivation through disease) or cause such problems (e.g. insufficient nutrient intake for maintenance and growth of the body). Expression of a normal behavioural pattern is associated with natural living, while a change in this pattern and expression of abnormal behaviour, such as tail biting, ear biting, excessive aggression, and stereotypies can indicate distress or frustration in animals due to their environment (McPhee & Carlstead, 2010). These abnormal behaviours are also associated with pain, if they are damaging for the animal itself or the recipient (Mench, 1998). Also other behaviours can indicate affective states of animals, for example, fear behaviour (Puppe et al., 2007) and play behaviour (Boissy et al., 2007; Yeates & Main, 2008). Furthermore, behaviour of pigs might also affect environmental and economic issues. Behaviours such as urinating and defecating affect ammonia emission and, therefore, influence the environmental performance of the farm (Blanes-Vidal et al., 2008; Groenestein et al., 2007). Behaviours such as tail biting and

feeding affect health and growth, and hence the productivity of a pig and the economic performance of a farm (De Haer et al., 1993; Smulders et al., 2006; Zonderland, 2010).

Although behaviours are considered as important indicators for welfare, they are often not easy to understand and should be interpreted cautiously. Several motivations can underlie a change in behaviour and the impact on welfare can be context dependent (Temple et al., 2011). The expression of behavioural patterns at farm level, and hence the related sustainability performance emerge from the complex interplay among a whole range of internal (e.g. genetic background, sex) and external (e.g. ventilation, housing, feeding, management) factors. Understanding how these internal and external factors affect pig behaviour improves our interpretation of behaviour as welfare indicator and deepens our insight in other sustainability issues.

### **1.2.1 Concepts of motivational systems**

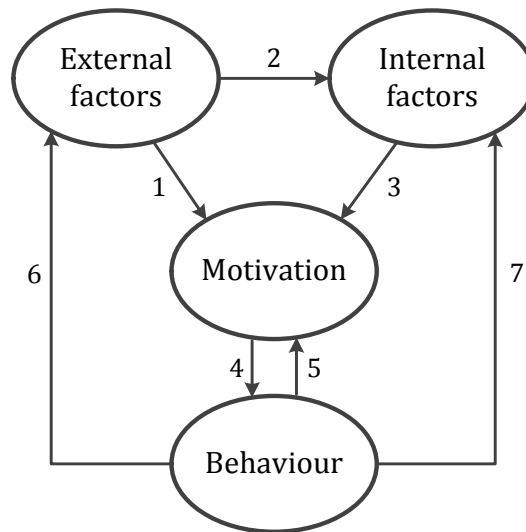
The dependency of behaviour on internal and external factors seems to vary. Whereas some behaviours, such as agonistic behaviour, seem to depend mainly on external factors, others, such as feeding behaviour, seem to depend more on internal factors. Specifically behaviours, such as nest-building behaviour and exploration behaviour in pigs, are internally driven as a species-specific 'behavioural need' independent from external factors and 'functional consequences of the activity' (Jensen & Toates, 1993). Many researchers have tried to understand the complex interaction between internal and external factors affecting behaviour in empirical studies, but were in most cases not able to sufficiently unravel all factors and to identify all important species-specific animal behaviours (Rushen & de Passillé, 2009).

Motivational systems are a proximate mechanism to explain how various factors interact and integrate in behaviour. Over time, several conceptual models have been developed that describe how motivational systems can affect animal behaviour (e.g. Hughes & Duncan, 1988; Lorenz, 1950; Wiepkema & Koolhaas, 1993). These models include different aspects of behaviour, such as set-points, feedback mechanisms and the role of internal and external factors (Jensen & Toates, 1993).

Jensen and Toates (1993, 1997) developed a conceptual model in which they integrate diverse aspects of these models (Figure 1). In their model, feedback mechanisms that down-regulate motivation through behaviour are essential. Negative and positive feedback mechanisms regulate processes to respectively start or stop the performance of a behaviour. These mechanisms prevent unnecessary switching 'dithering' between behaviours and ensure that behaviours last long enough to reach the functional goal of that behaviour (Mason & Bateson, 2009). Negative feedback can reduce motivation and can be caused, for example, by performance of the particular behaviour, performance of an alternative behaviour and passage of time (Hogan, 1997). In contrast, positive feedback increases motivation after start of a behaviour

and stimulates continuation of the behaviour (Mason & Bateson, 2009). This model can be exemplified with applying it to feeding behaviour. Internal factors in feeding behaviour can represent, for example, processing of feed in the stomach, hormonal circadian rhythms and the energy balance. External factors can represent the light-dark cycle and feed availability. The arrows in Figure 1 can then, for example, represent:

1. The dark-light cycle can affect the sleep-wake cycle and increase or decrease feeding motivation.
2. The dark-light cycle can affect hormonal circadian rhythms that affect the energy balance.
3. Deviation from the optimal energy balance and an empty stomach can increase feeding motivation.
4. Feeding motivation can cause feeding behaviour.
5. Proprioceptive feedback that feeding behaviour is performed can increase motivation (positive feedback) or reduce motivation (negative feedback).
6. Feeding behaviour can deplete the feed source.
7. Feed intake can affect the energy balance and stomach load.



**Figure 1.** A model of motivation underlying animal behaviour (adapted from Jensen and Toates (1997). Numbers in the model are explained in the text.

To translate internal and external factors and feedback mechanisms into motivation and behaviour, a model should include a mechanism that explains when motivation leads to expression of the behaviour. Hogan (1997) proposed a model with a general energy and threshold variable. Where the energy variable can be constructed from



both internal and external factors and affects motivation, the threshold level sets limits to the expression of a specific behaviour. Energy for feeding behaviour, for example, can increase when nutrient levels fall short and decrease when nutrient levels are supplemented by feed intake. The threshold for this behaviour can be affected by, for example, circadian rhythms that increase or decrease the threshold level at specific times. This model explains how behaviour occurs even though there seems to be no reason for it (e.g. in the absence of an external factor that would normally stimulate it), and in the contrary, how no behaviour occurs even though there seems to be a reason for (e.g. best time of the day).

Another important aspect in a model of behaviour is the consideration of competition between various motivations and behaviours, such as for feeding, drinking or fleeing. To include interactions among multiple motivational systems, the state-space approach can be used (McFarland & Sibly, 1975). In this approach, motivational levels will be compared to each other and compete for behavioural expression. The motivation with the highest priority will be performed until a certain lower limit is reached and other behaviours can be performed, or another incentive becomes higher in the meantime higher and inhibits the behaviour.

Motivational models are used to explain animal behaviours such as fighting behaviour (Payne & Pagel, 1996), affiliative primate behaviour (Puga-Gonzalez et al., 2009), dust bathing in hens (Hogan & van Boxel, 1993), and feeding behaviour in sheep (Sauvant et al., 1996). In pigs, examples of motivational models include fighting behaviour (Andersen et al., 2004) and social spacing behaviour (Stricklin et al., 1995). These models explain the causation of behavioural patterns. Although they are not explicitly meant to study animal welfare, they offer opportunities for this, for example, by addressing motivations and emotions of animals (Stricklin et al., 1995). Inability to cope with causal internal and external factors, and thus failure to perform motivated behaviours, may lead to stress and welfare problems (Jensen & Toates, 1997). Furthermore, understanding motivations underlying behaviour can help us in understanding abnormal behaviours and stimulating animals to perform behavioural patterns, which are beneficial to us and them (e.g. optimised feeding patterns) (Mason & Bateson, 2009).

### **1.3 Methodological approach**

As described above, to understand sustainability performance of pig production systems, a systems approach is necessary that takes both internal and external factors on motivation and behaviour into account as well as positive and negative effects of behaviour on welfare and other sustainability issues. Modelling the motivational system underlying behaviour and the consequences of this behaviour, will provide

insight in the relation of this behaviour with animal welfare and other sustainability issues.

So far, model studies focussed on understanding animal behaviour and underlying motivations, or on evaluating or predicting animal welfare on farm level without understanding motivations underlying behaviour. The integration of both research areas is missing, while this is essential to understand pig behaviour and related welfare. The challenge, therefore, is to integrate these two model approaches in a way that both underlying motivations as well as related welfare and other sustainability issues of behaviour can be analysed. This requires understanding of the system on various organisational levels and knowledge of multiple disciplines (e.g. ethology, physiology, and psychology) (Collins & Part, 2013).

To improve understanding of intensive systems on pig behaviour and to identify processes that are important in sustainability performance, a model should be dynamic and mechanistic. Dynamic models include variation in states of the system (e.g. variation of motivation over time) and mechanistic models explicitly include mechanistic processes that can cause this variation (e.g. interaction among internal and external factors) (Haefner, 2005). Especially for multidimensional issues such as welfare, these kind of models have high potential (Collins & Part, 2013).

Since behaviour and welfare can vary between individuals and interaction among individuals (e.g. aggression, tail biting behaviour) can affect the performance of a group, a model should also represent processes of individual animals. Agent-based models are especially suitable to study individual variation and interaction among individuals. Agent-based modelling is a simulation method in which individuals are programmed to behave autonomously based on a set of rules (Railsback & Grimm, 2012). It is a method that allows individual variation and interaction among individuals and with the environment. Due to these interactions, patterns can emerge on a higher level that can be compared with real life patterns. The strength of agent-based modelling is that it “unsimplifies” processes (individual variation and interaction is included), which are often difficult to include in other models (Railsback & Grimm, 2012).

Several motivational studies use agent-based modelling (or comparable modelling techniques) to gain better understanding of complex interactions between animal behaviour and the environment (e.g. Puga-Gonzalez et al., 2009; Stricklin et al., 1995). Although the use of agent-based modelling in understanding animal behaviour and assessing animal welfare has been limited so far, there seems to be much potential for further application (Asher et al., 2009). Agent-based modelling also has been used to study interactions between environmental regulation and nitrogen losses in pig systems (Happe et al., 2011), and disease risks for wild (Lange & Thulke, 2016) and domesticated pigs (Arruda et al., 2016). Given these experiences, agent-based

modelling appears to be a promising tool to simulate pig behaviour and sustainability performance in pig production systems.

## **1.4 Aims**

The aims of this thesis are:

- To assess whether agent-based modelling can increase our understanding of pig behaviour and underlying motivations.
- To apply agent-based modelling to increase our understanding of pig behaviour, and related animal welfare and productivity performance.

Tail biting behaviour and feeding behaviour were chosen as a case study in this thesis. Tail biting behaviour was chosen to represent a behaviour that has been intensively studied, but still is not well-understood and has major welfare implications. Feeding behaviour was chosen as a behaviour that is better (but not fully) understood and has implications for all three sustainability concerns. In addition, the motivation underlying feeding behaviour might also be important in tail biting behaviour.

## **1.5 Outline of this thesis**

The outline of this thesis is shown in Figure 2. It consists of four parts:

- 1) Exploring the use of agent-based modelling (Chapter 2).
- 2) Understanding internal factors and mechanisms underlying behaviour (Chapter 3 and 4).
- 3) Understanding external factors and mechanisms underlying behaviour (Chapter 5).
- 4) Analysis of individual variation and related behavioural and productivity performance (Chapter 6).

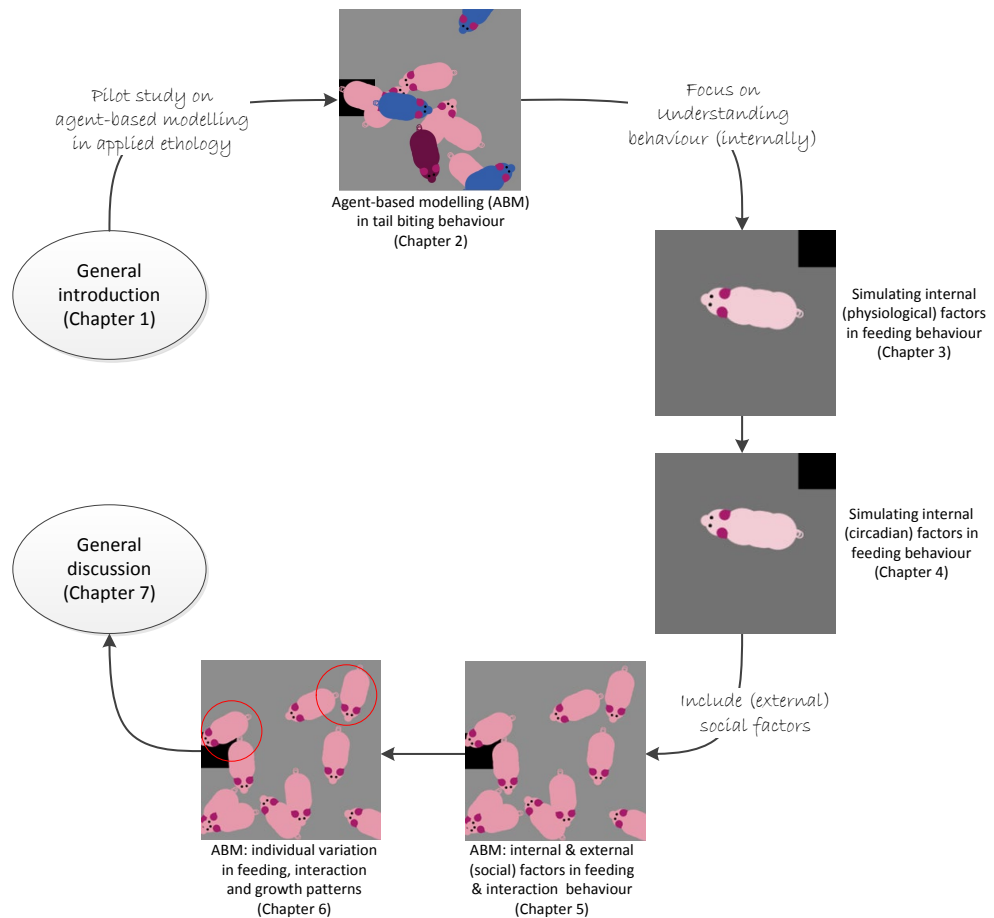
In the first part, Chapter 2, the use of agent-based modelling in applied ethology was explored, with tail biting behaviour as case study.

In the second part, Chapter 3 and 4, the internal factors and mechanisms underlying feeding behaviour of an individually housed pig were modelled. Chapter 3 focusses on feeding patterns of pigs during the entire growing/fattening period and metabolic and growth processes, such as energy absorption, energy use and protein and fat deposition. Chapter 4 focusses on feeding patterns of pigs within 24 hours and the effect of hormonal circadian rhythms.

In the third part, Chapter 5, the external factors and mechanisms underlying feeding and interaction behaviour of group-housed pigs were modelled.

In the fourth part, Chapter 6, individual variation in pigs and related behavioural and growth patterns were modelled.

In Chapter 7, the use of agent-based modelling for understanding pig behaviour, motivations underlying this behaviour, related welfare issues and productivity performance are discussed.



**Figure 2.** Outline of this thesis. Model development to understand behaviour in pigs.





## Chapter 2

# **Agent-based modelling in applied ethology: an exploratory case study of behavioural dynamics in tail biting in pigs**

Iris J.M.M. Boumans<sup>a</sup>, Gert Jan Hofstede<sup>b</sup>, J. Elizabeth Bolhuis<sup>c</sup>, Imke J.M. de Boer<sup>a</sup>, and Eddie A.M. Bokkers<sup>a</sup>

<sup>a</sup> Animal Production Systems group, Wageningen University, P.O. Box 338, 6700 AH Wageningen, the Netherlands

<sup>b</sup> Information Technology group, Wageningen University, P.O. Box 8130, 6700 EW Wageningen, the Netherlands

<sup>c</sup> Adaptation Physiology group, Wageningen University, P.O. Box 338, 6700 AH Wageningen, the Netherlands

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### **Abstract**

Understanding behavioural dynamics in pigs is important to assess pig welfare in current intensive pig production systems. Agent-based modelling (ABM) is an approach to gain insight into behavioural dynamics in pigs, but its use in applied ethology and animal welfare science has been limited so far. We used ABM in a case study on tail biting behaviour in pigs to explore the use of ABM in gaining more insight into emergent injurious pig behaviour and related welfare issues in intensive production systems. We developed an agent-based model in Netlogo 5.1.0 to simulate tail biting behaviour of pigs housed in conventional pens in groups of 10. Pigs in the model started as neutral pigs (not involved in biting incidents), but could change into a biter, victim, or both biter and victim. Tail biting behaviour could emerge when pigs were unable to fulfil their internal motivation to explore. The effects of a redirected exploratory motivation, behavioural changes in victims and preference to bite a lying pig on tail biting patterns were tested in our model. The simulations with the agent-based model showed that coincidence in development of a redirected exploratory motivation can lead to tail biting behaviour in pigs and can explain the strong variations in incidence of tail biting behaviour observed in conventionally housed pigs. Behavioural changes in victims and preference to bite a lying pig seem to be of minor importance in the causation of tail biting patterns. The behavioural time budget of a pig might be an important factor in predisposing pigs to or preventing them from becoming a tail biter or a victim. ABM showed to be useful in analysing behavioural dynamics and welfare issues. An advantage for ABM in applied ethology is the availability of data from empirical studies.

*Keywords:* tail biting behaviour; behavioural patterns; motivation; welfare; agent-based model; time budget.



## 2.1 Introduction

Current intensive pig production systems are subject to major sustainability concerns, including concerns about pig welfare (Averós et al., 2010; Krystallis et al., 2009). Welfare is a state of the animal of which behaviour is an important indicator (Duncan, 1998). Behaviour is dynamic and the result of a complex interaction between internal factors, such as behavioural needs and characteristics of pigs, and external factors, such as housing conditions and time of day (Jensen & Toates, 1993). Within the EU, fattening pigs in conventional intensive systems are generally housed in rather barren pens, on fully or partially slatted concrete floors, with a space allowance of 1 m<sup>2</sup> per animal or less (EFSA, 2007b). These housing conditions can lead to several welfare issues, such as tail biting and leg injuries (Averós et al., 2010; EFSA, 2007a). Many studies have demonstrated effects of specific adjustments in housing conditions on pig behaviour and other welfare indicators. For instance, housing enriched with rooting materials reduced severe tail biting in pigs (Van de Weerd et al., 2006). To understand the effect of housing on pig welfare, however, it is important to consider the interaction with other internal and external factors and their effect on behavioural dynamics in pigs.

One approach to gain insight into behavioural dynamics is agent-based modelling (ABM) (Railsback & Grimm, 2012). ABM can be used to analyse how pig behaviour emerges from a complex interaction of internal factors and external factors, and how behaviour can develop over time. Although several scientific disciplines, such as ecology and social sciences, commonly use ABM, the use of this method in applied ethology and animal welfare science has been limited so far (Asher et al., 2009; Collins & Part, 2013). ABM, however, has potential for use in these fields, since it can include individual variation and social interactions. Furthermore, ABM has the advantage that it can simulate experiments with many combinations of factors and repetitions, which would require many animals and be costly in real life (Asher et al., 2009). The aim of this study is to explore the use of ABM in applied ethology by using a case study of behavioural dynamics in tail biting in intensively housed pigs.

Tail biting behaviour in pigs is defined as biting and chewing (manipulating) the tail of another pig. It can be scaled from gentle to severe and may cause bleeding wounds and infections (D'Eath et al., 2014; Schrøder-Petersen & Simonsen, 2001). Tail biting behaviour can increase over time and lead to a tail biting outbreak (Zonderland et al., 2011b). Tail biting clearly has welfare consequences for the pig that is bitten. It however also has economic consequences for the farmer because pigs with wounds, infections and increased stress might grow less or even die (D'Eath et al., 2014; Schrøder-Petersen & Simonsen, 2001).

The causation of tail biting behaviour is not fully understood and is suggested to be multi-factorial (Moinard et al., 2003). Many risk factors for tail biting behaviour have

been identified on commercial farms, including housing conditions, such as lack of rooting materials and high stocking density, and pig characteristics, such as genetic background and poor health (Taylor et al., 2010). As current knowledge on risk factors is not sufficient to control tail biting behaviour under commercial conditions, Schröder-Petersen and Simonsen (2001) suggested that internal factors and behavioural mechanisms, under influence of external factors, should receive more attention.

Tail biting behaviour is an interesting case for exploring the use of ABM in applied ethology because an agent-based model allows including behavioural mechanisms and interaction with internal and external factors, and can indicate how these can lead to emergent behaviours such as tail biting. We developed an agent-based model on tail biting behaviour following the steps in the modelling cycle described by Grimm and Railsback (2005), which includes formulating research questions, choosing a model structure, implementing the model, and model analysis. In this paper we discuss the difficulties and opportunities of using ABM in applied ethology by presenting the development, analysis and results of the model on tail biting.

## **2.2 Theoretical framework on tail biting behaviour in pigs**

We used the pattern-oriented modelling (POM) strategy to develop a theoretical framework on tail biting behaviour in pigs. In POM, a model is developed to simulate observed patterns that characterise the system of interest (Grimm & Railsback, 2012; Grimm et al., 2005). If in an agent-based model similar patterns emerge that resemble those empirically observed, that model might contain the right mechanisms for the modelled problem (Grimm & Railsback, 2012). It would then count as an explanation of the causation of these patterns.

### **2.2.1 Patterns in tail biting behaviour**

Tail biting behaviour entailed on average about 0.07% of the behavioural time budget of a pig in a study with barren housed and tail docked pigs between 5 and 19 weeks of age (Bolhuis et al., 2005). The amount of tail biting behaviour, however, varies largely between studies and between pigs. In a study on barren housed and presumably undocked pigs of Beattie et al. (2005), for example, 43% of the pigs performed tail biting behaviour between 4 and 7 weeks of age, of which 21% spent less than 1.5% of their time on tail biting behaviour and 22% of the pigs spent 1.5% or more of their time on tail biting behaviour.

Tail biting behaviour can develop from a pre-injury stage without visual tail damage into an injury stage with injured and bleeding tails. Bleeding tails can lead to increased restlessness and more pigs engaging in the biting behaviour (EFSA, 2007b). Zonderland et al. (2008) observed an average duration of 7.5 days for development

from bite marks to a visible tail wound, but there was a large variation since in a few cases it also evolved within a day. The prevalence of any indication of tail damage in abattoirs ranges on average from 3% in docked pigs to 6-10% in undocked pigs (EFSA, 2007b).

Pigs can be categorised in biter, victim, both biter and victim or neutral (not involved in biting incidents). In barren housed and undocked pigs, 59-67% of the pigs was identified as neutral, 9-10% as biter, 20-29% as victim, and 3-5% as both biter and victim (Brunberg et al., 2011; Ursinus et al., 2014).

### **2.2.2 Explaining factors in tail biting behaviour**

The model should contain factors that explain the emergence of tail biting behaviour. We considered the following explaining factors in our model: a (redirected) exploratory motivation, behavioural changes in victims and a preference to bite a lying pig. These factors are further described below.

#### **2.2.2.1 A redirected exploratory motivation**

In this paper we focus on the two-stage type of biting behaviour, which is described in most papers (Taylor et al., 2010). Two-stage tail biting behaviour is suggested to start as a redirected exploratory behaviour, in which exploratory behaviour such as oral manipulation is directed to tails. Initially the behaviour causes no visible damage or distress to the victim, but it can turn into more forceful biting behaviour when the skin of a tail is damaged (Taylor et al., 2010). The lack of rooting materials is indicated as the main risk factor for redirecting exploration behaviour to tails of pen mates (Taylor et al., 2010). Although stress is not indicated as a cause in the two-stage type of biting behaviour by Taylor et al. (2010), it seems important in the causation of tail biting behaviour. Not being able to fulfil the behavioural need to explore is thought to be one of the main factors causing stress (Schrøder-Petersen & Simonsen, 2001). Stress might accumulate when multiple factors such as housing conditions, health or feed are suboptimal. Stress can increase the frequency and intensity of normal behaviour patterns, and might change normal behaviour into abnormal behaviour (Schrøder-Petersen & Simonsen, 2001). The question remains, however, why not all pigs in a group, exposed to the same conditions, perform tail biting behaviour if tail biting behaviour is caused by environmental factors or a motivation for oral manipulation (Beattie et al., 2005).

#### **2.2.2.2 Behavioural changes in victims and preference to bite a lying pig**

Since victims show little to no reaction to being tail bitten, the effect of tail biting behaviour on a victim in the pre-injurious stage seems limited (Taylor et al., 2010). Several studies, however, reported an increase in general activity (e.g. Statham et al.,

2009; Zonderland et al., 2011b) and changes in behaviour of tail biting victims before tail injuries occur. Future tail biting victims showed, for example, more daily feeding visits than pen mates or control pigs two to five weeks before a tail biting outbreak (Wallenbeck & Keeling, 2013), and a higher level in activity and posture changes than control pigs days before a tail biting outbreak (Zonderland et al., 2011b). This may suggest that victims of tail biting behaviour are affected by tail biting behaviour in the pre-injury stage, even though they do not show outward responses to a tail bite. It might be that victims internally build-up stress or unrest when being bitten, which can be behaviourally expressed at a later time. Biters do not seem to have a preference to bite the tail of a specific group mate (Zonderland et al., 2011a), although victims in the pre-injurious stage are often pigs that lie down (Taylor et al., 2010). This suggests that tail biting pigs have a preference for inactive pigs and being an inactive pig increases the risk of being a victim. If being bitten increases restlessness and activity in victims, it might reduce the risk of being victimised again. As a result the risk that other pigs become victims increases and this can explain why there are often more than twice as many victims than biters in groups.

### **2.2.2.3 Tail damage**

The point at which the skin of a tail breaks is indicated as the transition of non-damaging to damaging tail biting behaviour. This important point in time likely depends on the development of tail damage. It is not clear, however, how quickly a tail can develop from fully intact to severely damaged, from wound to inflammation, and eventually to healing or to death. There are indications that tail damage development in pigs is a cumulative process (Zonderland et al., 2011a). Biting characteristics such as frequency, strength and duration affect this development. What determines these biting characteristics, however, is unclear. Factors such as the level of motivation or stress, the rewarding effect of tail biting behaviour, reaction of the victim, and state of the tail (e.g. bleeding) are likely involved. More active and manipulative behaviour can be seen in groups with tail biting behaviour (Ursinus et al., 2014). A higher level of arousal in these groups could, for example, increase the motivation to explore and thereby lead to more tail biting behaviour (Zonderland, 2010).

### **2.2.3 Tail biting behaviour and research questions**

Based on the factors discussed above, we decided to model the dynamics in tail biting behaviour and the categorisation of pigs (neutral, biter, victim, or both biter and victim) before the injury stage. Tail damage was excluded from the model at this stage, as its development showed no clear pattern and several questions remained about factors involved in it.

We composed the following research questions:

1. Can a motivation to bite, driven by needs to explore or by stress, explain the patterns in incidence of tail biting behaviour?
2. Can this motivation turn initially neutral pigs into a biter, victim, biter and victim or neither of these?
3. What is the effect of behavioural changes in victims on these patterns?
4. What is the effect of a preference of biters biting the tail of a lying pig on these patterns?

### **2.3 Model description**

An agent-based model was developed in Netlogo 5.1.0 (Wilensky, 1999). The model simulates the behaviour of pigs (agents) housed in a conventional pen in a group of 10. Tail biting patterns emerge as a redirected behaviour based on internal motivation of pigs to bite (MOTIVATION) when exploratory needs cannot be fulfilled. The effect of MOTIVATION as sole factor causing tail biting behaviour and categorisation of pigs (research question 1 and 2) was tested in the reference setting of the model. The factors preference for biting the tail of a lying pig (PREFERENCE) and behavioural changes in victims (CHANGE) were tested in an extension of the reference setting (research question 3 and 4). The model and a detailed model description following the ODD (Overview, Design concepts, Detail) protocol (Grimm et al., 2006; Grimm et al., 2010) are available in the model library of the OpenABM website (<http://www.openabm.org>).

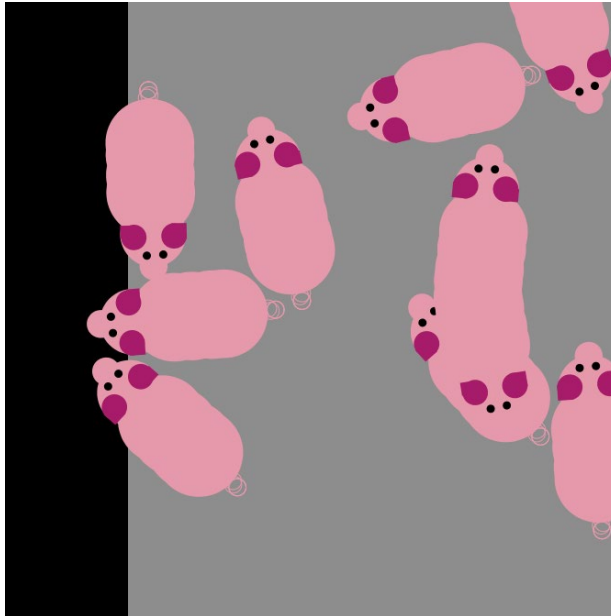
#### **2.3.1 Model environment and agents**

The environment in the model represents a barren pen with a concrete floor and enough feeding spaces, with ad libitum feed for all pigs to feed simultaneously (Figure 1). We assumed that in the housing system, besides lack of opportunities to fulfil the motivation to explore, no stressors were present. The model allowed pigs to feed in the assigned area and move around randomly using the whole pen. In accordance with commercial conditions, a specific lying area was not assigned and, therefore, pigs could lie down anywhere in the pen. Pigs in the model started as neutral pigs, but changed into a biter, victim, or both biter and victim when they were bitten or biting.

#### **2.3.2 Model processes**

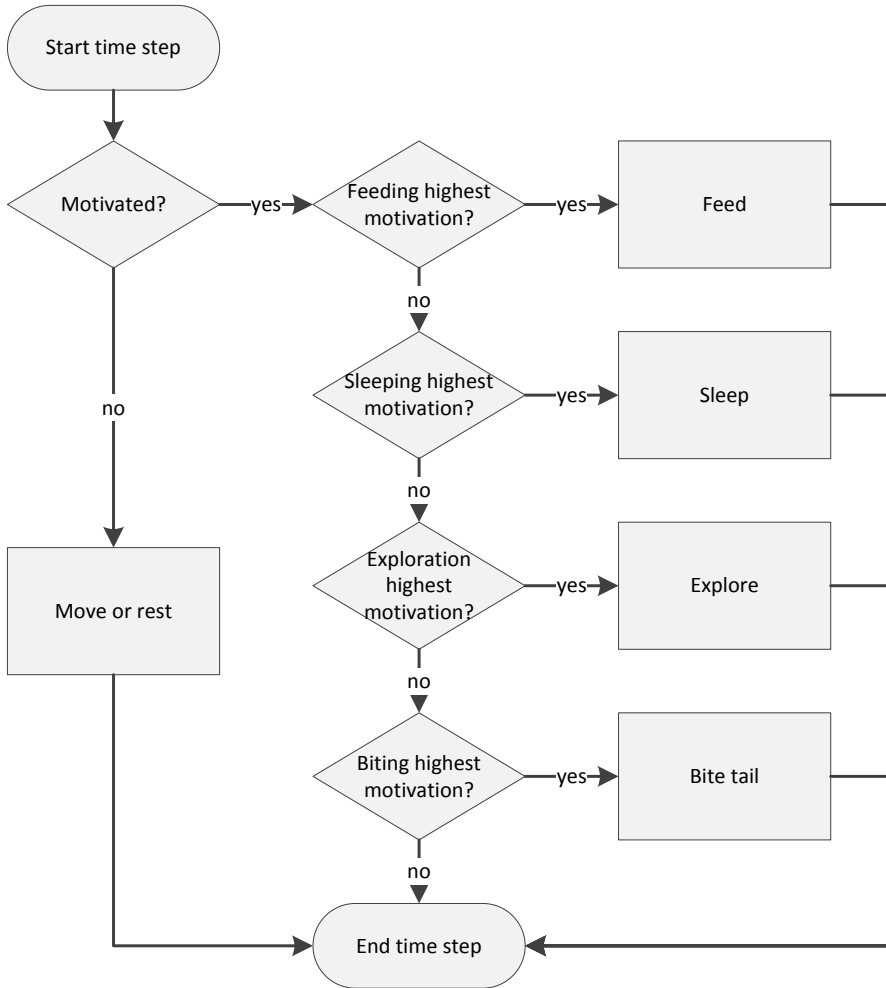
Behaviour of pigs kept in barren intensive housing systems, in their active period during daytime, consists of about 70-80% lying behaviour and 20-30% active behaviours, such as feeding and exploring (e.g. Bolhuis et al., 2005a). Pig behaviours in the model were sleeping, resting, feeding, exploring, moving and tail biting. These behaviours represented 93% of the daily time budget of pigs in the study of Bolhuis et

al. (2005a). Behaviours were not synchronized and could randomly occur during the day. Pigs did not interact with each other, except when a pig was tail biting. Tail biting pigs selected the nearest pig (in the reference setting) or (if present) the nearest inactive (resting or sleeping) pig as a victim (if PREFERENCE was included).



**Figure 1.** Graphical interface of the model. The model represents a barren pen with concrete floor (grey), feeding space (black) and ten pigs.

Four internal states affected the behavioural time budget of a pig: feeding drive, sleeping drive, exploration drive, and (redirected) biting drive. Each time step, pigs (in a random order) checked their internal states. When an internal state was above a threshold, pigs became motivated to perform the behaviour related to the internal state (Figure 2). Threshold levels for feeding, sleeping and exploration drive were zero, meaning that these states caused a behavioural motivation when above zero. Motivations were calculated as the difference between the internal state and the fixed threshold level. To represent individual variation among pigs, the threshold for biting drive varied randomly per pig, based on a normal distribution with a mean of 0.5 and standard deviation of 0.05. When pigs were not motivated, they randomly moved or rested based on a probability (respectively 0.14 and 0.86). This probability was calibrated to correspond to empirically observed behavioural time budgets of pigs (e.g. Bolhuis et al., 2005a).



**Figure 2.** Flowchart of the processes for performing a behaviour in the model for one pig each time step.

Internal states in the model changed each time step depending on the performed behaviour (Table 1). All behaviours affected the feeding and sleeping drive. Resting, feeding and moving behaviour increased the exploration drive, while sleeping behaviour decreased it. Since the barren environment lacked opportunities to fulfil the motivation to explore, exploring did not decrease the exploration drive, but increased the biting drive. The biting drive decreased with sleeping behaviour (to a minimum of zero) and with tail biting behaviour. Being bitten had no effect on the victim (in reference setting), or increased the biting drive and decreased the sleeping drive of a victim, representing supposed effects on increased activity and restlessness (if CHANGE was included). The feedback values of behaviours on internal states were

calibrated to cause behavioural time budgets corresponding to empirical observations.

**Table 1.** Feedback values of performed behaviours on internal states of pigs in the model per time step.

Internal states	Feedback values of behaviours (per time step)					
	Sleep	Rest	Feed	Explore	Move	Bite tail
<i>Performing pig</i>						
Exploration drive	-0.10	0.17	0.05	-	0.17	-
Feeding drive	0.09	0.09	-1.11	0.18	0.18	0.18
Sleeping drive	-0.20	0.17	0.21	0.21	0.21	0.21
Biting drive	-0.09	-	-	0.28 <sup>2</sup>	-	-0.09
<i>Receiving pig</i>						
Biting drive	-	-	-	-	-	0.05 <sup>1</sup>
Sleeping drive	-	-	-	-	-	-0.20 <sup>1</sup>

<sup>1</sup> If impact of tail biting on a victim was included in the simulation. <sup>2</sup> This is a rounded number. In the model the number 0.276 was used (which was necessary to balance the increase of biting drive during exploration with the decrease of biting drive during sleeping).

In the initial state of the model, values for internal states were set to a random value based on a normal distribution with a mean of 0 (for sleeping drive and exploration drive), and -0.4 (feeding drive) and a standard deviation of 0.25. These values were chosen after several simulation runs to correspond to the average levels of the internal states during the simulation. Biting drive was set to zero in the initial state, assuming that pigs have no motivation to bite tails in the morning after a night of mainly sleeping.

We selected a time step of one minute in our model. It was assumed that this time step is short enough to represent one tail biting incident and the effect on biting motivation of pigs. Total simulation time was chosen to represent a light period of twelve hours (720 minutes) in which pigs are more active. Tail biting behaviour seems to occur especially in this period (Schrøder-Petersen & Simonsen, 2001).

## 2.4 Model analysis

The effect of three factors was tested in four scenarios:

1. MOTIVATION
2. MOTIVATION + PREFERENCE
3. MOTIVATION + CHANGE
4. MOTIVATION + PREFERENCE + CHANGE



The effect of MOTIVATION (research question 1 and 2) was tested in scenario 1. The effect of additional factors (research question 3 and 4) was tested in various combinations in scenario 2, 3 and 4. Each scenario was repeated 100 times.

The sensitivity of simulation results to parameter changes was tested in a local sensitivity analysis. Parameter values in the model were varied one at a time with an alteration of 50% (Table 2). Each simulation of a parameter change was repeated 100 times. The sensitivity to parameters was tested in the reference setting of the model (scenario 1), except for parameters that were related to CHANGE on a victim, these parameters were tested in an extended setting of the model (scenario 4). In addition, equal initial internal states and equal thresholds for the biting drive were simulated in the reference setting to test the sensitivity of model results to variation between pigs.

**Table 2.** Sensitivity analysis of average time spent on tail biting behaviour and the distribution of pigs into biting categories (in scenario 1 and 4) to parameter settings in the model<sup>1</sup>.

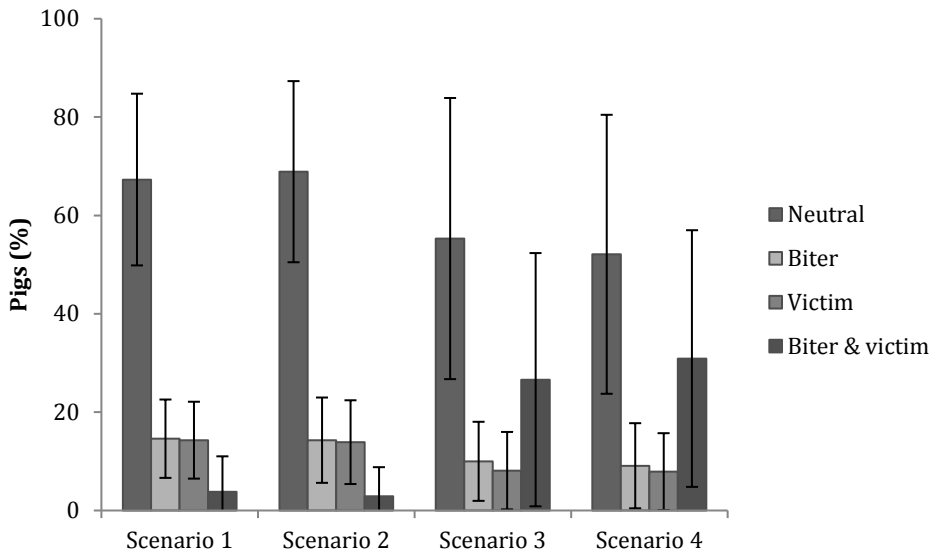
Parameter	Reference value	Parameter alteration (%)	Tail biting behaviour (%)	Neutral (%)	Biter (%)	Victim (%)	Biter & victim (%)
<i>Scenario 1<sup>2</sup></i>			0.03	67.3	14.6	14.3	3.8
<i>Effect of number of pigs and duration<sup>3</sup></i>							
Number of pigs	10	-50	0.03	66.6	15.6	15.0	2.8
		+50	0.02	70.1	14.0	13.7	2.2
Simulation steps	720	-50	0.02	84.6	7.6	7.5	0.3
		+50	0.02	59.3	17.3	17.3	6.1
<i>Effect of tail biting behaviour on biter<sup>3</sup></i>							
Decrease biting drive	0.09	-50	0.03	68.7	13.9	13.7	3.7
		+50	0.03	68.8	14.3	14.2	2.7
Biting threshold	0.5	-50	0.79	0.0	0.6	3.7	95.7
		+50	0.00	98.2	0.9	0.9	0.0
Random deviation	0.05	-50	0.02	69.4	14.4	14	2.2
biting threshold		+50	0.03	64.1	15.5	16.9	3.5
<i>Scenario 4<sup>2</sup></i>			0.07	52.1	9.1	7.9	30.9
<i>Effect of tail biting behaviour on victim<sup>4</sup></i>							
Increase biting drive	0.05	-50	0.06	59.0	9.5	8.0	23.5
		+50	0.07	56.2	7.2	5.3	31.3
Decrease sleeping drive	0.20	-50	0.04	62.5	13.4	13.6	10.5
		+50	0.20	36.9	3.1	1.5	58.5

<sup>1</sup> Values are averages of 100 simulations. <sup>2</sup> Results of the model with initial parameter values. <sup>3</sup> Tested in scenario 1 (with motivation to bite as only factor included). <sup>4</sup> Tested in scenario 4 (all factors included).

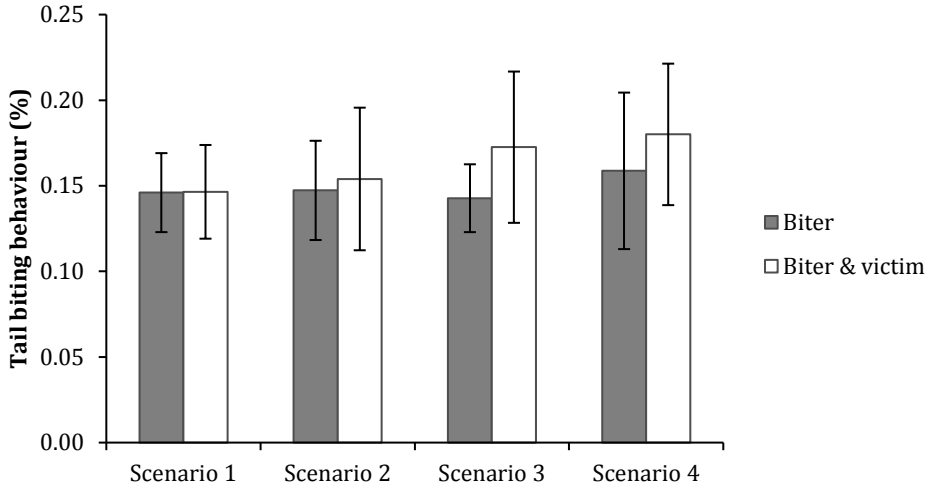
## 2.5 Model results

### 2.5.1 The effect of MOTIVATION on tail biting patterns (research question 1 and 2)

The average behavioural time budget of the pigs in scenario 1 consisted of 49% sleeping, 23% resting, 16% exploring, 9% feeding, and 4% moving. The average tail biting behaviour in the time budget of pigs was 0.03%, within a range of 0% to 0.08% tail biting behaviour. On average, 67.3% of the pigs remained neutral, 14.6% became biter, 14.3% became victim, and 3.8% became both biter and victim (Figure 3). Pigs that were tail biting (18.4% of the pigs) spent on average 0.15% of their time on tail biting behaviour (Figure 4).



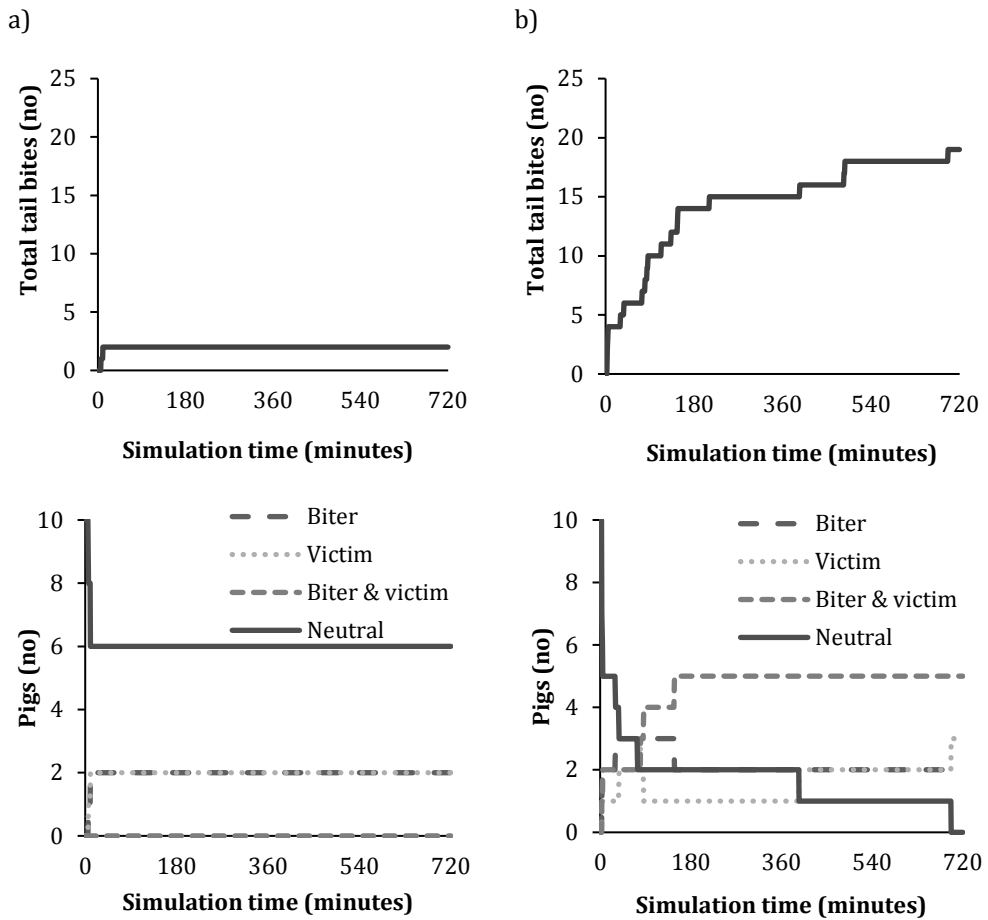
**Figure 3.** The average and standard deviation of distribution of pigs into tail biting categories (neutral, biter, victim or biter and victim) in four scenarios. Simulations of each scenario were repeated 100 times.



**Figure 4.** The average and standard deviation of time spent on tail biting behaviour of pigs that are biter or biter and victim in four scenarios. Simulations of each scenario were repeated 100 times.

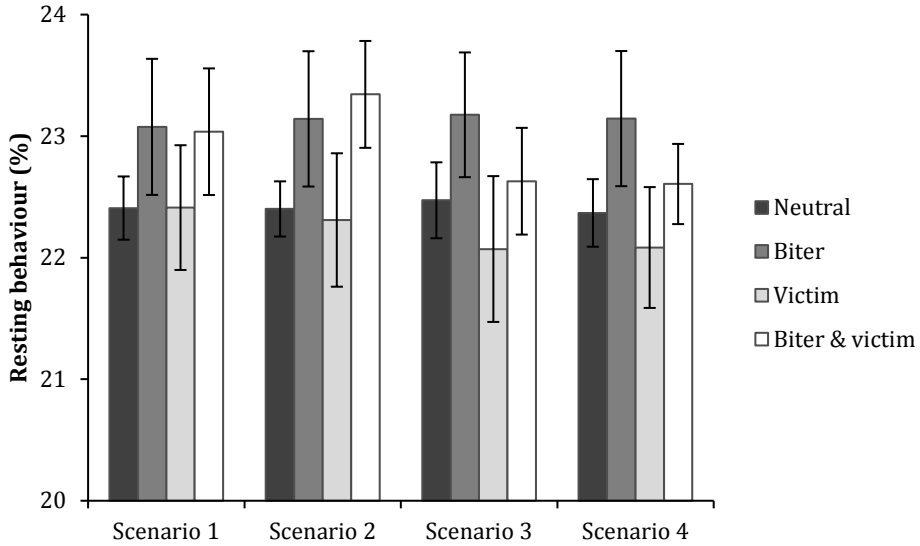
### 2.5.2 The effect of additional factors on tail biting patterns (research question 3 and 4)

Adding CHANGE to the model (scenario 3 and 4) had no clear effect on the average behavioural time budget of pigs. The average tail biting behaviour in the time budget in scenario 3 and 4 was 0.06% (range 0% to 0.24%) and 0.07% (range 0% to 0.26%), respectively. To illustrate the variation in patterns between simulations, a run with a low level of tail biting behaviour (Figure 5a) and a run with a high level of tail biting behaviour (Figure 5b) is displayed. CHANGE decreased the number of neutral pigs and increased the number of pigs that were both biter and victim (Figure 3). In scenario 3, 55.3% of the pigs remained neutral, 10.0% became a biter, 8.1% became a victim, and 26.6% turned into both biter and victim. Biters spent on average 0.14% of their time on tail biting behaviour while pigs that were both biter and victim spent 0.17% of their time on biting (Figure 4). Irrespective of the included factors, tail biting pigs spent more time on resting behaviour than non-biting pigs. When CHANGE was included, victims spent least time on resting behaviour (Figure 6). In contrary, tail biting pigs spent least time on moving behaviour in all scenarios (3%), whereas victims spent most time on moving behaviour when CHANGE was included (4%). Differences between behavioural time budgets of biting and non-biting pigs were very small with about 0.5% for resting and moving behaviour and about 0.1% for feeding, exploring and sleeping behaviour.



**Figure 5.** Development of tail biting incidents and categorisation of pigs in model scenario 4 during a run with a) 2 biting incidents (0.03% tail biting) and b) 19 biting incidents (0.26% tail biting).

Adding PREFERENCE to the model (scenario 2 and 4) had no clear effect on the average behavioural time budget of pigs and on the average level of tail biting behaviour. The average tail biting behaviour in scenario 2 (0.03%, within a range of 0% to 0.07%) was similar to scenario 1 (0.03%, within a range of 0% to 0.08%). And the average tail biting behaviour in scenario 4 (0.07%, within a range of 0% to 0.26%) was similar to scenario 3 (0.06%, within a range of 0% to 0.24%). Adding PREFERENCE slightly increased the number of neutral pigs and decreased the number of pigs that were both biter and victim in scenario 2 compared to scenario 1 (respectively into 68.9% and 2.9%), whereas the opposite effect occurred in scenario 4 compared to scenario 3 (respectively into 52.1% and 30.9%) (Figure 3).



**Figure 6.** The average and standard deviation of time spent on resting behaviour of pigs in the four tail biting categories (neutral, biter, victim or biter and victim) in four scenarios. Simulations of each scenario were repeated 100 times.

### 2.5.3 Sensitivity analysis

The sensitivity analysis showed that in scenario 1 tail biting behaviour was mainly affected by the biting threshold (beyond this threshold biting drive caused biting motivation) (Table 2). In scenario 4 (with CHANGE and PREFERENCE included), a higher decrease of sleeping drive in a victim increased the average percentage of tail biting behaviour. In general, when the percentage of tail biting behaviour increased, the percentage of neutral pigs decreased and the percentage of pigs that were both biter and victim increased.

When initial internal states and biting thresholds of pigs were set equal, the average tail biting behaviour in the time budget of pigs was 0.01%, within a range of 0% to 0.04% tail biting behaviour. On average, 81.0% of the pigs remained neutral, 9.4% became biter, 8.8% became victim, and 0.8% became both biter and victim.

## 2.6 Discussion

The case study was suitable to explore and exemplify the use of ABM to gain insight into tail biting patterns of pigs. We developed an agent-based model that shows how the hypothesised role of biting motivation can cause observed patterns in tail biting behaviour.

### 2.6.1 Explaining tail biting patterns

ABM was used to test factors that might explain patterns of tail biting behaviour before the injury stage. A redirected behaviour, driven by exploratory needs or stress, is the most hypothesised factor for causing two-stage tail biting behaviour (Taylor et al., 2010).

The agent-based model in our study showed that a redirected motivation to bite can lead to tail biting behaviour in pigs and can explain the varying emergence of tail biting behaviour observed in conventionally housed pigs. The diversity in tail biting patterns emerging from the same initial situation, showed that coincidence caused tail biting behaviour in some simulations, but not in all. This explains why not all pigs in a group perform tail biting behaviour, even if they can all become motivated to bite tails. The sensitivity analysis showed that the amount of tail biting behaviour in the model was sensitive to the biting threshold parameter. Decreasing the biting threshold with 50%, caused an increase of tail biting behaviour of more than 200% (from 0.03% to 0.79%). This effect is major, but it reflects tail biting behaviour in reality since the amount of tail biting behaviour can vary largely between studies and between pigs (e.g. Beattie et al., 2005; Bolhuis et al., 2005a). Thus, this threshold is important in the model and might represent a real life mechanism.

We hypothesised that behavioural changes in victims and a preference to bite a lying pig might affect the number of victims and explain the empirically observed ratio of biters to victims (about 1:3) (Brunberg et al., 2011; Ursinus et al., 2014), since it decreases the chance that a victim with increased activity is bitten again. The model, however, did not support this hypothesis since in all scenarios most simulations finished with slightly more biters than victims. Having a preference for biting the tail of a lying pig seems to be of little importance in tail biting behaviour, since neither incidence of tail biting behaviour nor the distribution of pigs in tail biting categories was affected when PREFERENCE was added to model. The sensitivity analysis showed that increasing the biting threshold parameter by 50% could increase the ratio of biters and victims to 1:4, but in that case the remaining pigs all turned into both biter and victim. It might be that the difference in time spent on activity between victims and other pigs was too small in our model (in total a decrease in resting and sleeping behaviour of less than 1% of the time budget), and therefore had hardly any affect. The sensitivity analysis showed that further decreasing the sleeping drive of a victim indeed increased the fraction of victims, but the ratio biter and victim remained 1:1.

When CHANGE was included in the model, being bitten provoked no immediate reaction in a victim pig, but decreased the sleeping motivation and increased the biting motivation of that victim. This increased the time victims spent on active behaviours and increased the risk that a victim became a biter as well. The number of pigs that were both biter and victim increased substantially to about 30%, which is

higher than the empirically observed 3 to 5% (Brunberg et al., 2011; Ursinus et al., 2014). The sensitivity analysis showed that the values chosen for the decrease of sleeping drive and (to a lesser extent) the increase of biting drive in a victim affected this. Lower values reduced the number of pigs that were both biter and victim, however, did not change the ratio biter and victim. This suggests that behavioural changes in victims was not an import factor in the causation of non-damaging tail biting behaviour. Another explanation can be that our model assumptions did not represent the correct mechanisms for behavioural changes in a victim. Increased activity in victims is observed in empirical studies (e.g. Statham et al., 2009; Zonderland et al., 2011b) and it might also be that being bitten, for example, should have affected activity in the model via moving motivation instead of sleeping motivation.

That the model was not able to simulate the empirically observed ratio of biters to victims indicates that another factor is important in the distribution of pigs into four tail biting categories. For instance, predisposition of pigs to become a biter or victim. Pigs in the model only differed slightly by random variation in initial internal states, biting thresholds and random moving and resting behaviour. The sensitivity analysis showed that varying the initial internal states and biting thresholds between pigs affected the distribution of pigs into categories only minimally. The risk of becoming a tail biter, however, was related to the random chance of performing moving or resting behaviour. Tail biting pigs in the model spent more time on resting behaviour and less time on moving behaviour than neutral pigs or victims. Resting and moving behaviour affected the motivations of other behaviours, whereby moving behaviour increased sleeping and feeding motivation more than resting behaviour did. Since sleeping behaviour decreased the biting motivation and feeding behaviour increased exploration motivation less than the other behaviours did, more moving behaviour was beneficial for having a lower biting motivation. The relation between tail biting behaviour and resting behaviour is a result of the assumed effects of behaviours on internal states of pigs. Since the relations between behaviours and internal states were not validated and feedback values were based on a calibration, the model might have been incorrect or too sensitive to changes in the behavioural time budget of a pig. If these assumptions are correct, however, the model shows that the behavioural time budget of a pig affects biting motivation and might be important in the predisposition to become a biter and/or victim. Pig characteristics that are identified as risk factors, such as breed, gender, growth (D'Eath et al., 2014), might be related to differences in behavioural time budgets of pigs. Performing more exploratory behaviour, for example, might increase the risk of becoming a biter (D'Eath et al., 2014; Larsen et al., 2016), while performing motivated behaviours such as sleep, might decrease a tail biting drive and thereby the risk of tail biting behaviour. In addition, biting behaviour in the model was assumed to decrease biting drive, but it might be that at some point (e.g. with high stress levels) biting behaviour might also

increase the biting drive further and could cause a forceful or obsessive kind of tail biting behaviour (Taylor et al., 2010). Although empirical studies showed that some behaviours seem to have predictive value for tail biting behaviour (e.g. activity level and explorative behaviour), the relation between temporal development of these behaviours and tail biting behaviour needs further investigation (Larsen et al., 2016). Animal behaviour is a result of a complex interaction between internal and external factors. If the combination of behaviours and underlying factors contributes to emergence of tail biting behaviour, this explains why so many factors are found to affect tail biting behaviour. Due to interactions, their combined effect can lead to different levels of tail biting.

### **2.6.2 Use of ABM in applied ethology**

ABM showed to be useful for gaining more insight in emergent pig behaviour. The use of ABM in the case study of tail biting behaviour facilitated in bringing knowledge together and identifying knowledge gaps. Developing an agent-based model requires including behavioural decision-making of an agent and the processes involved that explain patterns at system level. Performing analysis from an agent (pig) perspective helped identifying gaps in knowledge, such as mechanisms underlying the strength and duration of tail biting behaviour or the selection of a victim.

ABM has no standard method for model development (Asher et al., 2009). Many decisions were made during development of the model, such as the hypothesis to test and which behaviours, factors, relations and assumptions to include. Although the flexibility of ABM to construct a model is an advantage, it also increases the risk of mistakes (Asher et al., 2009). If a model contains many assumptions on unknown relationships and processes, it has a high level of uncertainty and may give the wrong impression about the real causation of the behaviour. Furthermore, a model with many parameters can be difficult to analyse since the number of potential combinations can become very large. A model can become unreliable when relationships among variables are not understood (Asher et al., 2009).

We developed a simple agent-based model that showed how ABM can be useful for gaining more insight in potential important mechanisms underlying behavioural dynamics in tail biting. Understanding pattern causation through the dynamics of factors is a key value of ABM. This has been demonstrated in several other studies on animal behaviour such as the role of self-organisation in flocking behaviour in birds (Hildenbrandt et al., 2010), fighting and grooming in primates (Puga-Gonzalez et al., 2015) and social dynamics in group feeding patterns of farmed chicken (Collins et al., 2011; Collins & Sumpter, 2007). Understanding how a behaviour is caused can require considerable detail in processes (Boumans et al., 2015; Tichit et al., 2009). Using ABM for further analysis of tail biting behaviour can require including more parameters (e.g. stress, individual differences), parameter values and relationships among them,



which can increase the risk of mistakes further (Asher et al., 2009). We believe, however, that ABM can be very useful in a stepwise approach. Insights from the current model can be used for directing new studies on tail biting behaviour to potentially interesting information, such as the relation between tail biting behaviour and other behaviours. The model could be further developed when new knowledge becomes available. Housing or pig characteristics that contribute to various behavioural time budgets of pigs, for example, could be added step by step.

An advantage for ABM in applied ethology is the availability of data. Compared to ecological or social models on animal or human behaviour, farm animals such as pigs are kept in highly standardised and controlled environments. Pigs often have, for example, limited space, a fixed group size, and are fed diets with known nutrients, and exposed to controlled ambient temperatures. Many of these conditions have been measured and included in study results. The availability of this data makes it easier to find multiple and specific patterns for model development and to validate model results with empirical results.

## **2.7 Conclusion**

The agent-based model showed that coincidence in development of a redirected exploratory motivation can lead to tail biting behaviour in pigs and can explain the varying emergence of tail biting behaviour observed in conventionally housed pigs. Behavioural changes in victims and preference to bite a lying pig seem of little importance in the causation of non-damaging tail biting behaviour. The behavioural time budget of a pig, however, might be an important factor in predisposing pigs to or preventing them from becoming a tail biter or a victim. ABM facilitates bringing knowledge together and identifying gaps. Thus it acts as a hypothesis-generating method that can prompt new questions. Furthermore, it can give new insights in important factors in the causation of observed behavioural patterns. ABM can be useful in analysing behavioural dynamics and welfare issues in applied ethology, provided that sufficient knowledge is available on the causation of the behaviour and sufficient data from empirical studies is available to validate output of the model. It can also contribute to understanding behaviour in a stepwise approach, whereby insights from a model can direct new empirical research and the findings can be used for further model development. An advantage for ABM of pigs in applied ethology is the availability of data. Compared to other disciplines, such as ecology, relative much and precise data is available of behaviour of farm animals.

## **Acknowledgements**

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# Chapter 3

## Understanding feeding patterns in growing pigs by modelling growth and motivation

Iris J.M.M. Boumans<sup>a</sup>, Eddie A.M. Bokkers<sup>a</sup>, Gert Jan Hofstede<sup>b</sup> and Imke J.M. de Boer<sup>a</sup>

<sup>a</sup> Animal Production Systems group, Wageningen University, P.O. Box 338, 6700 AH Wageningen, the Netherlands

<sup>b</sup> Information Technology group, Wageningen University, P.O. Box 8130, 6700 EW Wageningen, the Netherlands

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### **Abstract**

Feeding is an essential behaviour for body maintenance in pigs and closely related to their growth and productivity performance. Mechanisms underlying feeding behaviour in pigs are still unclear. Understanding these mechanisms can provide valuable insights into the complex interactions among various factors affecting feeding behaviour and help to improve growth and productivity of pigs. The aim of this study was to increase our understanding of internal causation and development of short-term feeding patterns in a pig, and the relation between feeding patterns and productivity of a pig during the growth period. We developed a mechanistic simulation model that represents an individually housed growing pig. The model integrates knowledge from physiology and ethology, and combines growth with a behavioural decision model based on motivation. Combining growth with behaviour allowed exploring the development of a pig over time, in particular the causation of growth and feeding patterns over a 24 h period and during the entire growing period. Physiological factors, affected by pig and feed characteristics, are important internal factors controlling feeding behaviour. Model output included short-term feeding behaviours in pigs (e.g. meal size, meal frequency and meal duration), and growth characteristics (e.g. energy use, body weight gain). The model yielded feeding patterns that were validated against empirical data. This modelling study provided insight in how growth and motivation explain the development of feeding patterns of an individually housed pig over time. Pig and feed characteristics affected the motivation to reach a desired level of daily feed intake. Without feeding restrictions, pigs adapted feeding patterns to reach this daily feed intake without affecting growth. The developed model is suitable to further study mechanisms underlying feeding behaviour and performance of group-housed pigs.

*Keywords:* pig feeding behaviour; meal patterns; motivation; growth; agent-based model.

### 3.1 Introduction

Feeding is an essential behaviour for body maintenance in pigs and closely related to their growth and productivity performance (Nyachoti et al., 2004). The amount of feed consumed directly affects the level of nutrient intake (Nyachoti et al., 2004), whereas the distribution of meals over the day affects the utilisation of nutrients (Batterham & Bayley, 1989; De Haer & de Vries, 1993b). Improving feed intake to optimize growth and productivity is still a major goal in pig production (e.g. Kanis, 1990; Rauw et al., 2006; Thingnes et al., 2012).

Feed intake results from the complex interaction of a number of factors. Multiple external factors are known to affect feed intake in pigs, such as dietary composition (Brouns et al., 1994), ambient temperature (Quiniou et al., 2000), group housing (Bornett et al., 2000a), and environmental stimuli (Beattie et al., 2000). Feed intake, however, also differs among individuals kept under similar conditions (Bornett et al., 2000a; Nielsen, 1999), due to a number of internal factors, e.g. genotype and sex (De Haer & de Vries, 1993a), body weight (Quiniou et al., 2000), physiological stage of development (NRC, 2012), and health (Williams et al., 1997).

Although much is known about the effects of the aforementioned external and internal factors on feeding, it is still unclear which underlying mechanisms are responsible for the observed feeding patterns, such as daily feed intake, meal frequency and meal size. Understanding the underlying mechanisms of feeding patterns in pigs can provide valuable insights into the complex interactions between various factors and help to improve the growth and productivity of pigs.

Several mechanistic models have been developed to simulate feed intake and daily growth in pigs. These models include, for example, feed composition and nutrient partitioning (e.g. De Lange, 1995; De Lange et al., 2003), environmental aspects such as stocking density and temperature (e.g. Yoosuk et al., 2011), or animal characteristics such as initial body weight, growth potential, and ability to cope with social stressors (e.g. Wellock et al., 2004). These models, however, do not include short-term feeding patterns, such as meal frequency, meal size, meal duration, and between-meal intervals. Models that do include short-term pig feeding patterns (e.g. Lewis & McGlone, 2008; Morgan et al., 2000) are empirical (regression) equation models, which do not model mechanistic effects on feeding patterns, which are essential to gain more insight into mechanisms underlying feeding patterns.

This study is the first step of a larger research project, in which we want to gain more understanding of feeding patterns in pigs and the role of interactions among individuals in one pen. We first want to understand internal processes controlling feeding behaviour, before we include social interactions among pigs. Therefore, the aim of this study was to create a model that would increase our understanding of

internal causation and development of short-term feeding patterns in a pig and the relation between feeding patterns and productivity of a pig during the growth period. In the case of an individual pig housed in a stable environment with ad libitum feed, we hypothesized that feeding patterns emerge from metabolic processes and ethological processes. Our model, therefore, included a constant interaction between growth and behaviour, caused by motivation, and affected by feed and pig characteristics. Combining growth with motivation allows studying the development of growth and feeding patterns in pigs over a 24 h period and during the whole growing period.

In this study, we used an agent-based model, which assists with the understanding of emergent behaviour resulting from interactions among individuals in a specific environment (Asher et al., 2009; Railsback & Grimm, 2012). We selected this type of model here because it meets the goal of the larger research project. Similarly, no attempt was made to simplify the processes included in the model, because these might become important when more than one agent is introduced in the model.

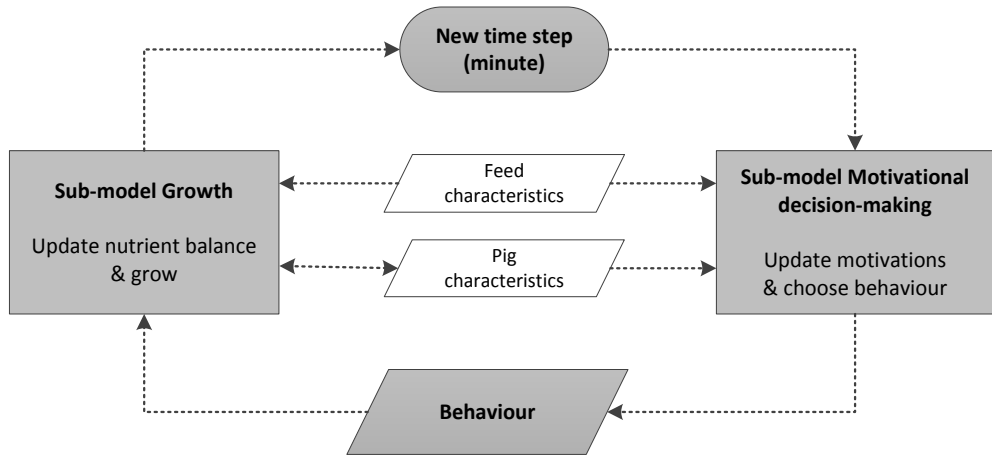
For model validation, results were compared with empirical data from literature. In addition, a local sensitivity analysis (Railsback & Grimm, 2012) was performed to assess how individual parameters in the reference settings affected model output and which parameters and conditions were important for the model results.

## **3.2 Model description**

### **3.2.1 Process overview**

The simulation model was constructed and implemented in the computer program Netlogo version 5.0.3 (Wilensky, 1999). The model represented one individually housed growing pig in a conventional pen, with ad libitum access to water and commercial dry feed, which met the nutrient requirements for maintenance and growth of the pig. Pig behaviour emerged from the interaction of two sub-models (Figure 1). In the sub-model called 'Motivational decision-making', the pig updated its four motivational states: feeding motivation, resting motivation, drinking motivation, and exploring motivation. These motivational states simultaneously affected its decision per time step to perform a specific behaviour, or (when motivational states were not high enough) remaining lying or standing. The chosen behaviour affected the energy use and feed intake of the pig, which subsequently changed its nutrient balance and growth, modelled in the second sub-model called 'Growth'. The outcome of the sub-model Growth was input again into the first sub-model. This interaction was modelled in time steps of one minute, adding up to days, as a continuous cycle over the entire growing period of 120 days. Each day (1440 minutes, 24 h) was modelled with a light period from 08:00 till 19:00 h, and a dark period in the

remaining hours. This reflected a common light regime and complied with the EU legislation requirements of a minimum of 8 h of light per day.



**Figure 1.** Overview of general processes in the model. Pig behaviour is caused by motivation, which is affected by pig characteristics, feed characteristics and the sub-model Growth. Arrows indicate causal relationships in the model.

**Table 1.** Input and output variables in the model.

Input variables	Output variables
<i>Pig characteristics</i>	<i>Feeding behaviour</i>
Sex	Feed intake (g/day)
Initial body weight (kg)	Meal frequency (no/day)
Initial body protein weight (kg)	Meal size (g/meal)
Mean body protein deposition (g)	Meal duration (min/meal)
Minimum body lipid to body protein ratio	Feeding rate (g/min)
	Meal interval time (min)
	Feeding time (min/day)
<i>Feed characteristics</i>	<i>Growth</i>
Digestible energy content of the diet (kJ/g)	Body weight gain (g/day)
Dietary protein content (g/kg)	Energy use (kJ/day)
Apparent protein availability	Body weight (kg)
Dietary amino acid content (g/kg)	Empty body weight (kg)
Apparent amino acid availabilities	
Diet digestion duration (min)	
Diet palatability	

Model output variables were the feeding and growth patterns of one pig (Table 1). Feeding patterns were calculated based on the behavioural decisions of the pig at each minute during the day. A meal started at a time step when the pig performed feeding behaviour and ended at the time step when it stopped feeding. Meal duration was calculated as the number of successive minutes that the pig was feeding for. Meal size

was the multiplication of meal duration with feeding rate per minute. On this basis, average interval time between meals, average meal frequency, total feeding time and total feed intake were calculated per day.

Model input variables on pig and feed characteristics are given in Table 1. Feed had a value for energy content, protein content and availability, digestibility, and palatability. The modelled pig was either a gilt, barrow or male, with a genotype effect based on a mean body protein deposition curve and a minimum body lipid to body protein ratio. Simulations started with a pig at 70 days of age, weighing approximately 27 kg.

### **3.2.2 Sub-model: Motivational decision-making**

The decision-making process of a pig to perform a given behaviour in the model was based on motivations. To let the pig autonomously decide on when and how to feed, a comprehensive motivational system for the causation of feeding motivation was included. In addition, to allow the pig to change its behaviour during a 24 h period and to model the effect on metabolic energy use, (less comprehensive) motivational systems for resting, drinking, and exploring were included.

#### **3.2.2.1 Causation of feeding motivation**

Feeding motivation and feedback mechanisms can be used to explain the interaction and integration of factors that control feeding behaviour (Day et al., 1998). Causation of feeding motivation in pigs was modelled analogous to work by Sauvant et al. (1996) on feeding decisions in sheep. Feeding motivation was a balance between feeding drive and satiation (Figure 2). Feeding drive increased feeding motivation, whereas satiation reduced feeding motivation: the pig was motivated to feed when its feeding drive was higher than its satiation. Two types of internal factors controlling feeding behaviour are often described: metabolic-homeostatic and cognitive-hedonic factors (Berthoud & Morrison, 2008; Johnson, 2013). Metabolic-homeostatic factors concern energy and nutrient levels within an animal (Johnson, 2013) and were, in this study, included as instantaneous factors (e.g. instant energy balance) affecting satiation, or daily factors (e.g. daily energy balance) affecting feeding drive. Cognitive-hedonic factors concern liking and wanting food and environmental cues (Berthoud & Morrison, 2008), and were here included as diet palatability and diurnal rhythm, affecting the feeding drive. Technical details of the causation of feeding motivation in the model are described in appendix A.1.

Feeding motivation can increase or decrease via feedback mechanisms. These mechanisms prevent unnecessary switching between behaviours and ensure that behaviours last long enough to reach the functional goal of a behaviour (Mason & Bateson, 2009). Positive feedback increases motivation when performing the related





### 3.2.2.2 Causation of other motivations

Besides feeding motivation, the pig in the model had the motivation to rest, explore and drink. These other motivations for behaviours often accompany feeding motivation. An increased feeding motivation will increase exploratory behaviour (rooting) and decrease lying behaviour (Day et al., 1995), whereas drinking behaviour often occurs around feeding behaviour (Bigelow & Houpt, 1988). Furthermore, these other behaviours can affect the energy use of a pig, which in turn can affect its growth and feeding motivation. Therefore, although less detailed as feeding motivation, motivations to rest, explore and drink were also included in the model. Causation of these behavioural motivations was based on motivational theory that includes an energy variable and threshold variable (Hogan, 1997). The energy variable represents an internal build-up of energy (drive) to perform a certain behaviour. The threshold variable limits the performance of the behaviour by requiring a minimum level of energy. In case the energy variable for resting behaviour exceeded its threshold level, for example, the pig became motivated to perform resting behaviour. The value of energy variables increased gradually each minute and decreased when the related behaviour was performed, as mentioned in the Lorenz model (described in Mason & Bateson, 2009). The value of threshold variables depended on the related behaviour and the time of day (Table 2). The fixed values for increase and decrease of energy variables each minute (Table 2) were calibrated to obtain common behavioural time budgets of pigs. At the start of the model, initial values of energy variables were set to a random value based on a normal distribution with a mean corresponding to the threshold value and a 10% standard deviation. Growing pigs in barren housing on average lie down for over 80% of their 24 h time budget, whereas feeding behaviour occupies approximately 10% of their time budget, and standing and drinking behaviours occupy approximately 8% of their time (Gonyou et al., 1992). Pigs feed, drink and stand mostly during their active (=light) period (Gonyou et al., 1992). In this period, barren housed growing pigs spend over 70% of their time lying, approximately 10% feeding and drinking and 15% exploring (Bolhuis et al., 2005a). Energy variables were modelled in such a way that absence of motivations could occur. Without sufficient motivation, a pig remained in the position (standing or lying) of the last behaviour. This prevented that the time budget of pigs in the model was fixed. Furthermore, this could represent a possible mechanism underlying the observed high amount of lying behaviour of pigs in conventional housing systems, which is that lying behaviour occurs due to resting motivation but is extended due to absence of stimuli.

**Table 2.** Input parameters and fixed values in the model for causation of motivations to drink, explore or lie down.

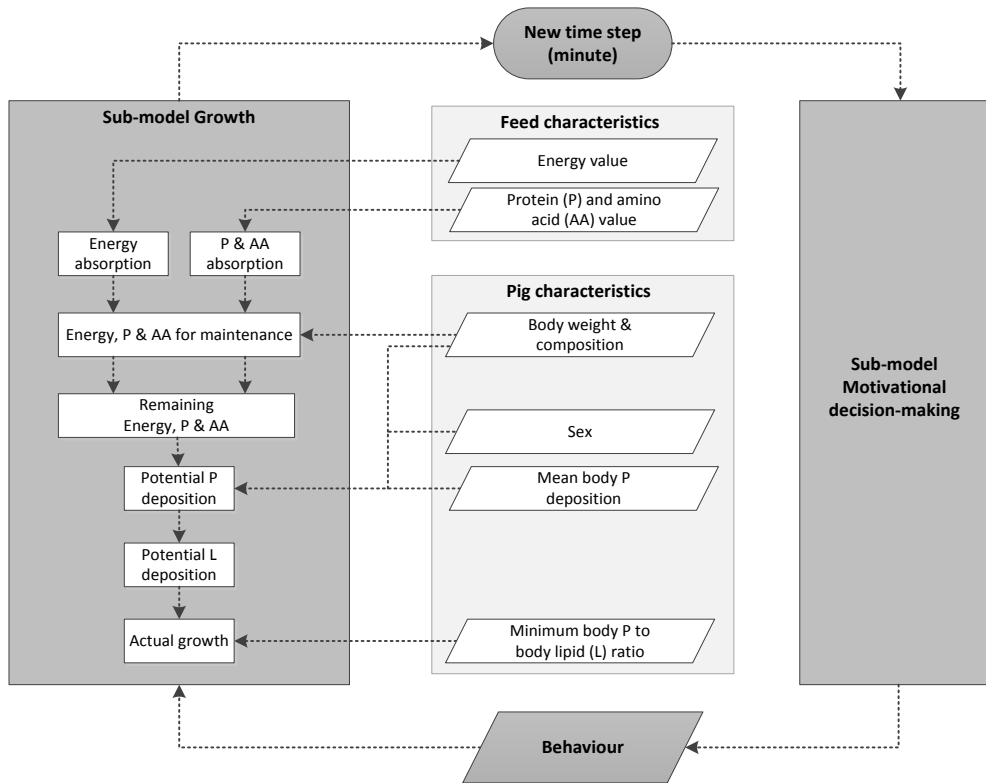
Variables	Values		
	<i>Resting</i>	<i>Drinking</i>	<i>Exploring</i>
<i>Threshold variables</i>			
Light period (08:00 to 19:00 h)	0.25	0.25	0.25
Dark period (19:00 to 08:00 h)	0.20	0.30	0.30
<i>Energy variables (change per minute)</i>			
Energy level increase when behaviour not performed	0.033	0.001	0.007
Energy level decrease when behaviour performed	0.021	0.279	0.258

### 3.2.2.3 Behavioural decision-making

Behavioural decision-making is modelled by the state-space approach (McFarland & Sibly, 1975). This approach implies that the behaviour related to the highest motivation will be performed until another motivation becomes higher or a certain threshold is reached. A pig in the model makes a decision each minute to act on the highest motivation (when above zero). When no motivation is above zero, the pig performs no behaviour, but remains in the position of its last behaviour (standing or lying). When a pig chooses to feed, it first determines its feeding rate, which is based on a preferred feeding rate affected by palatability of the feed and satiation of the pig (technical details in appendix A.2).

### 3.2.3 Sub-model: Growth

The sub-model Growth was based on the mechanistic pig growth model by de Lange (1995) on nutritional partitioning and growth in the pig. The time step in this model was converted from days to minutes and growth was included as a function of digested feed per minute, which allowed growth as a factor to affect feeding motivation during the day. Figure 3 shows how absorption and use of nutrients from digested feed results in a new body composition and body weight (BW) each minute. Switching to a time step of one minute allowed for negative growth to occur if required nutrients were extracted from the body when nutrient absorption from digested feed was insufficient for body maintenance. Input parameters for this sub-model are listed in Table 3, growth output parameters are listed in Table 1.



**Figure 3.** Schematic overview of the sub-model Growth (based on De Lange, 1995), and the interaction with the sub-model Motivational decision-making, behaviour, pig characteristics and feed characteristics each minute. Arrows indicate causal relationships in the model.

The relatively simple mechanistic model by de Lange (1995) contains the essential functions to predict growth (Black & de Lange, 1995; De Lange, 1995), but has inadequate assumptions on feed intake, energy use, and the effect of genotype on growth for use in a dynamic simulation model (Black, 1995). Equations for calculating feed intake and energy requirements in the model of de Lange (1995) were replaced by mechanistic results (feed intake, digested feed and energy use) of the sub-model Motivational decision-making. For the effect of genotype on growth more dynamic processes on protein deposition (PD) were included (see appendix A.3 for technical details).

**Table 3.** Input parameters and (initial) values in the model for body maintenance and growth.

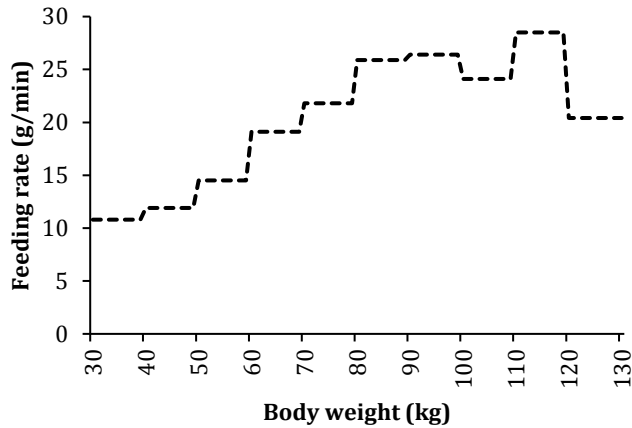
Parameter	Value
<i>Growth pigs</i>	
Initial body protein weight (kg) <sup>1,2</sup>	4
Initial body weight (kg) <sup>2</sup>	27
Minimum body lipid to body protein ratio <sup>1</sup>	1
Mean body protein deposition <sup>2</sup>	137, 133, 151 g/day for gilts, barrows and males respectively
<i>Diet composition and digestibility<sup>3</sup></i>	
DE content diet (kJ/g)	14.2
Dietary amino acid content Lysine (g/kg)	11
Dietary amino acid content Methionine (g/kg)	3
Dietary amino acid content Methionine + Cystine (g/kg)	6
Dietary amino acid content Threonine (g/kg)	6
Dietary amino acid content Tryptophan (g/kg)	2
Dietary amino acid content Isoleucine (g/kg)	5
Dietary protein content (g/kg)	132
Apparent amino acid and protein availabilities <sup>4</sup>	0.82

<sup>1</sup> De Lange, 1995. <sup>2</sup> NRC, 2012. <sup>3</sup> Values were formulated to meet dietary requirements of growing pigs with body weight 50-75 kg and mean body protein deposition rate of 155 g/day based on apparent ileal digestible basis of the diet as described in Table 16-3A in NRC, 2012. <sup>4</sup> Based on average ileal digestibility of amino acids in pig diets from Sauer and Just (1979) in Moughan (1995).

### 3.3 Results

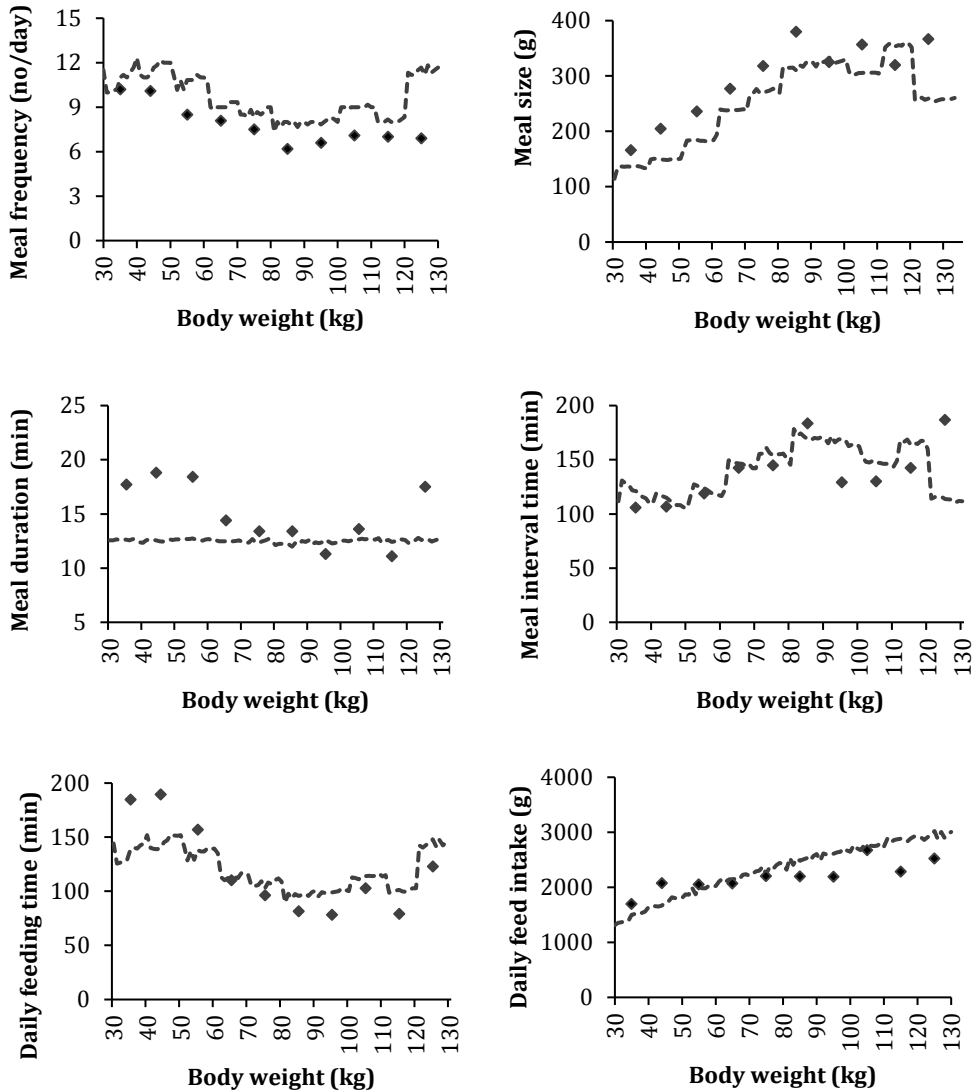
#### 3.3.1 Empirical validation of simulated feeding patterns

To validate the model, model output was compared with the empirical study of Bigelow and Houpt (1988) on feeding patterns of pigs. Bigelow and Houpt (1988) studied the feeding patterns of six individually housed female Yorkshire pigs, increasing in BW from 10 to 130 kg. Pigs were kept at a constant temperature of 22-23°C, and obtained a high quality pelleted feed of 1.72 Mcal/kg net energy (which is assumed to be 13 kJ DE/g) by pressing a panel. Lights were on from 07:00 till 19:00 h. To imitate these experimental settings in the model, the variables *sex*, *temperature*, *light period*, *dark period*, and *DE content diet* were adjusted to fit the empirical data of Bigelow and Houpt (1988). The development of feeding rate in pigs in the study of Bigelow and Houpt (1988) did not follow a linear function like the equation in our model, which was computed based on mechanistic processes (equation 15 in appendix A.2). To fit the study of Bigelow and Houpt (1988), the equation for feeding rate in our model was replaced by the mean values of feeding rate observed in their empirical study (Figure 4).

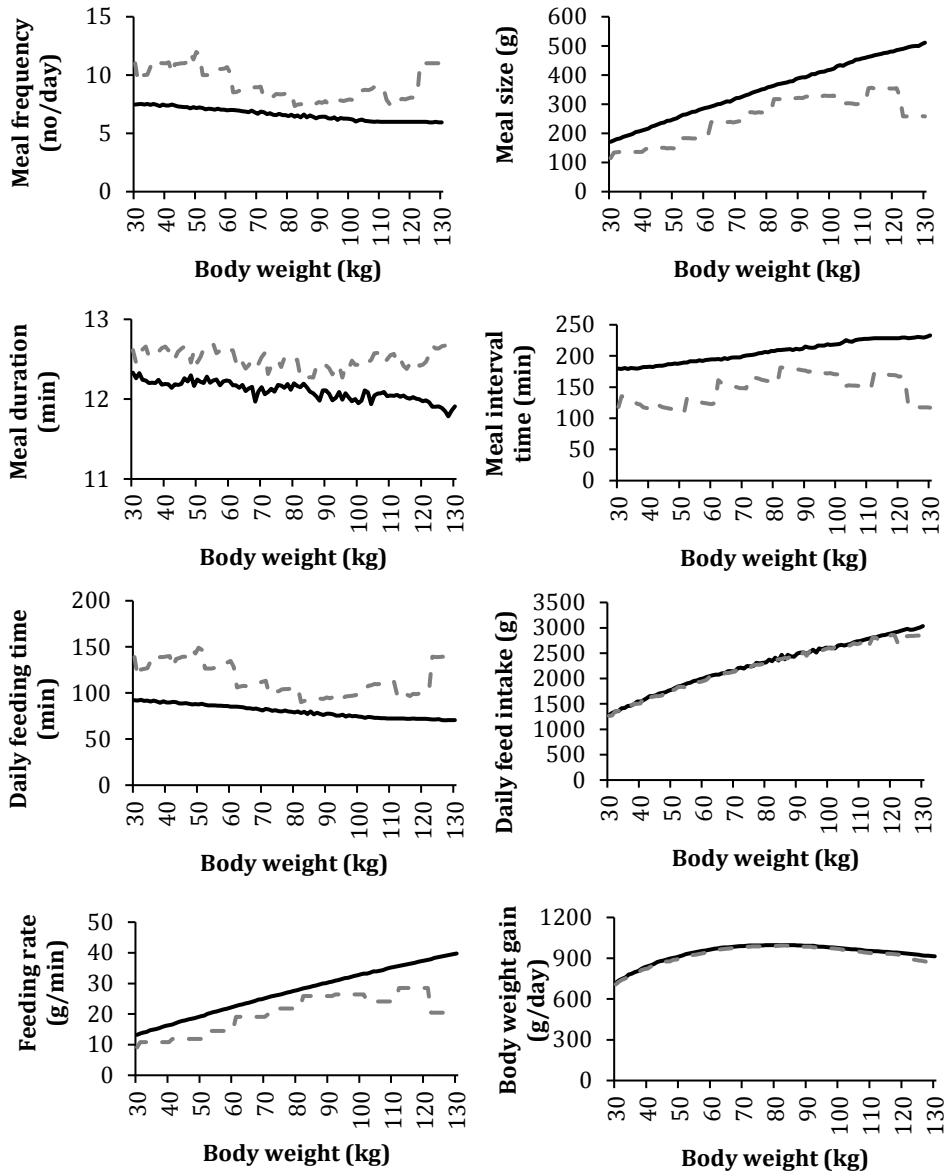


**Figure 4.** Feeding rate in the model based on mean values of feeding rate per body weight category of pigs from the study of Bigelow and Houpt (1988).

Figure 5 shows the comparison of empirically measured feeding patterns of pigs in the study of Bigelow and Houpt (1988) with the simulated feeding patterns in our model. In the empirical data, meal frequency decreased as BW increased, whereas meal duration tended to decrease (Bigelow & Houpt, 1988). Meal size and interval time between meals increased until pigs reached about 80 kg BW, whereas daily feeding time seemed to decrease until 80 kg BW (Bigelow & Houpt, 1988). Patterns of meal frequency, meal size, interval time between meals, and feeding time resulting from the model corresponded to empirical results until 120 kg BW. After 120 kg, meal size, meal frequency and interval time between meals showed some deviation. Meal duration in the model was relatively constant, while the empirical data of Bigelow and Houpt (1988) showed more variation in meal duration.



**Figure 5.** Validation of the model by comparing empirical feeding patterns based on feeding data (in which they excluded small feeding bouts of less than 10% of the average meal size) of six female Yorkshire pigs in experimental data of Bigelow and Houpt (1988) (◆) with results of 6 simulation runs of one gilt with a feeding rate adjusted to the data of Bigelow and Houpt (1988) in the model (---).



**Figure 6.** The effect on feeding patterns and body weight gain of two different types of feeding rates in the model: feeding rate based on the preferred feeding rate and affected by palatability and satiation (—) and the mean feeding rate values as observed in the empirical study of Bigelow and Houpt (1988) (- - -). Simulation runs of one gilt were repeated 50 times for each type of feeding rate with use of the reference parameter values.

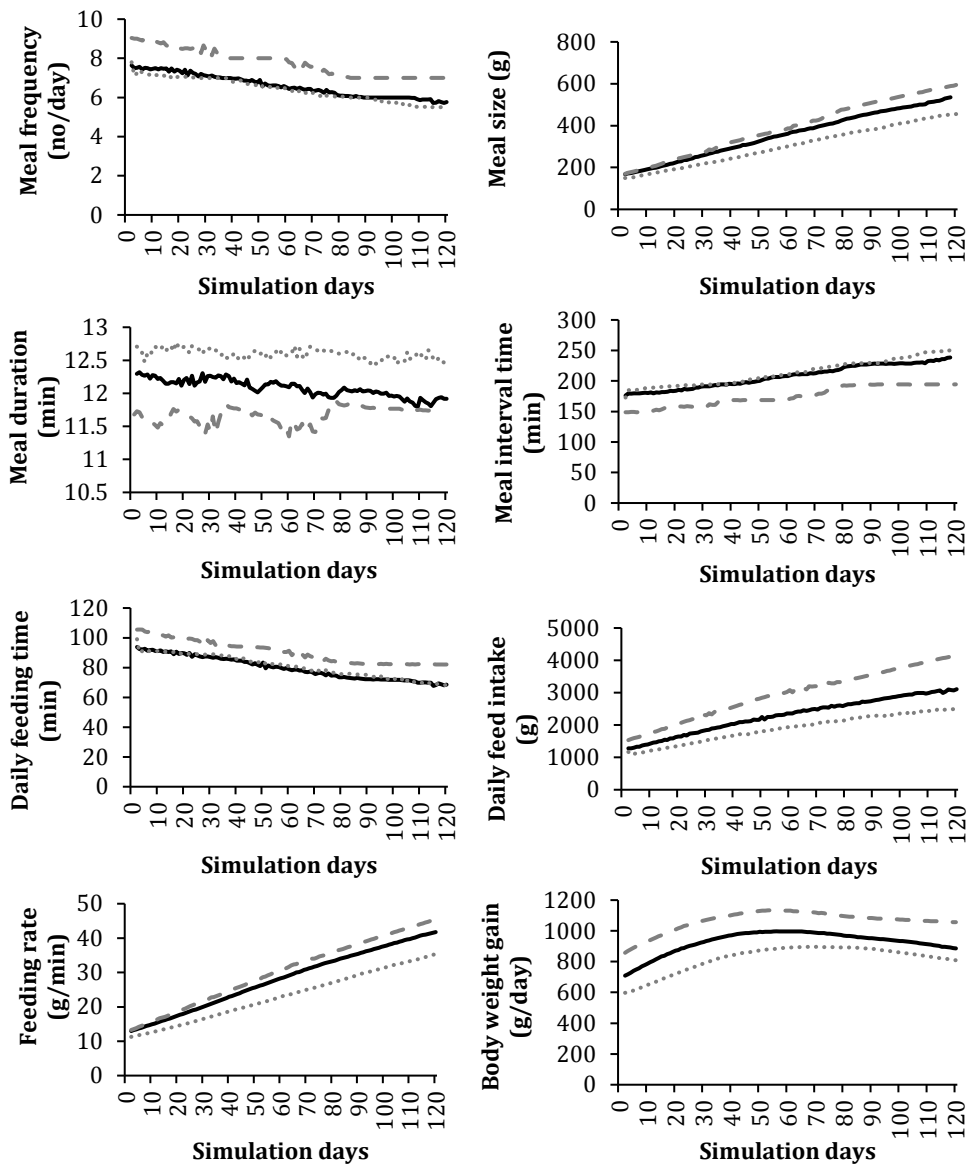


### **3.3.2 The effect of feeding rate on feeding patterns and growth**

Adjusting the feeding rate to the empirical values of Bigelow and Houpt (1988) was needed to reproduce feeding patterns reported in their study. We compared, therefore, model results based on empirical values of Bigelow and Houpt (1988) with results using the preferred feeding rate (equation 15 in appendix A.2). Figure 6 shows that feeding rate affects meal frequency, meal size, meal duration, meal interval time and feeding time. Feed intake and BW gain did not show a clear response. BW gain of pigs was slightly lower for empirical values compared with modelled values at the end of the simulation period.

### **3.3.3 Sensitivity analysis**

The sensitivity analysis involved varying the values of main parameters individually by 20% above (S+) or below (S-) their reference value. Table 4 shows the parameters included and their values used in the analysis. Final BW, mean daily feed intake, mean meal size and mean meal duration were chosen to represent the effect of parameters on growth and feeding patterns. Feed intake, and to a lesser extent final BW, was mainly affected by Diet\_palatability, Response\_to\_light and Digestion\_duration. Meal size and meal duration were mainly affected by Reinforcement\_feeding\_motivation, and to a lesser extent by Diet\_palatability. Figure 7 shows the effect of Diet\_palatability on all feeding patterns and BW gain. Decreasing Diet\_palatability had a limited effect on meal frequency, meal interval time, and feeding time, while increasing Diet\_palatability had an effect on all feeding patterns.



**Figure 7.** The effect of diet palatability on the development of mean feeding patterns and daily body weight gain. (— Reference setting, --- +20%, ..... -20%). Simulation runs of one gilt were repeated 50 times with use of reference parameter values and use of the model feeding rate equation.

**Table 4.** Sensitivity analysis of final body weight, mean daily feed intake, mean meal size and mean meal duration after 120 days of simulation<sup>1</sup>.

Parameter (reference value)	Variation final body weight (%) <sup>2</sup>		Variation mean feed intake (%) <sup>2</sup>		Variation mean meal size (%) <sup>2</sup>		Variation mean meal duration (%) <sup>2</sup>	
	S <sup>+</sup>	S <sup>-</sup>	S <sup>+</sup>	S <sup>-</sup>	S <sup>+</sup>	S <sup>-</sup>	S <sup>+</sup>	S <sup>-</sup>
<i>Feed characteristics</i>								
DE content diet (14.2 kJ/g)	5.5	-3.9	-5.5	13.8	2.7	-7.3	-1.6	0.2
Dietary amino acid content Lysine (11 g/kg)	0.0	-0.6	0.0	-0.5	0.0	-0.7	-0.1	0.1
Dietary total protein content (132 g/kg)	-1.0	-3.2	-0.4	-2.8	-0.6	-3.9	0.0	0.1
Diet palatability (0.85)	12.0	-9.2	28.6	-18.0	9.3	-15.6	-3.4	4.3
<i>Physiological factors</i>								
Response to light (0.7)	10.8	-7.6	26.3	-16.5	-8.1	3.4	-1.8	0.1
Response to darkness (0.5)	1.1	-1.0	1.9	-1.1	-0.7	0.9	-1.3	2.9
Reinforcement of feeding motivation (0.4)	0.4	-0.3	0.8	-0.7	18.4	-18.8	18.7	-19.1
Digestion duration (1230)	-3.9	7.4	-8.2	17.1	-6.7	4.5	1.3	-2.7
<i>Pig characteristics</i>								
Minimum body lipid to body protein ratio (1)	0.9	-0.9	0.9	-0.9	1.2	-1.1	0.0	0.1
Mean protein deposition gilts (137 g/min)	6.5	-8.6	2.8	-4.1	4.2	-5.8	0.0	0.1

<sup>1</sup> Simulation runs of one gilt were repeated 50 times with use of reference parameter values and use of the model feeding rate equation. <sup>2</sup> Parameter values were altered by 20% above their reference value (S<sup>+</sup>) or 20% below (S<sup>-</sup>). Sensitivity was calculated as output change from the reference output in percentage.

### 3.4 Discussion

Our model aimed at understanding the development of feeding patterns and related growth of individual pigs, which required the inclusion of relatively comprehensive mechanisms. To understand how feeding behaviour is controlled, a model requires considerable detail in the processes (Tichit et al., 2009). We included variables on the level of detail that was necessary to integrate motivation, behaviour and growth. The variable energy absorption, for example, affected both growth and motivation in the short and long term. Additionally, we expect that including this level of detail in our model is important for its future use, when more agents (i.e. more pigs) are to be included. Interactions among agents can affect processes underlying pig decisions on different levels. Competition for feed among pigs, for example, can increase the attractiveness of the feed, the feeding drive of a pig, or increase motivations other than feeding, such as avoiding fights or showing synchronised behaviours.

The validation showed that model predictions for the development of feeding patterns over time were comparable to the empirical data of Bigelow and Houpt (1988), except

for meal duration. Meal duration showed little variation in the model compared to the empirical study. The low variation can be explained by the parameter *Reinforcement\_feeding\_motivation*. This parameter was a theory-based parameter and no clear evidence for a value was available. A dynamic parameter value, based on the state of the animal (e.g. body weight or hunger level), would have been best, but such a value would have increased complexity and uncertainty in the model. Therefore, a fixed and calibrated value for *Reinforcement\_feeding\_motivation* was chosen. Although the fixed parameter caused a less accurate pattern of meal duration in the model, the effect on other feeding patterns and performance was limited. The sensitivity analysis showed that an increase of *Reinforcement\_feeding\_motivation* prolonged meal duration and increased meal size, whereas feed intake and BW were not affected. This corresponds to the suggestion of Nielsen (1999) that animals adjust their feeding patterns to reach a certain level of energy intake. Thus, when meal duration and meal size decreased, the pig increased its meal frequency in order to reach the same feed intake. Despite the inability to vary meal duration, the model still showed consistency with the empirical results of Bigelow and Houpt (1988) on meal frequency, meal size, interval time between meals and feeding time until the pig weighed 120 kg. The deviation in feeding patterns after 120 kg could be a result of the low variation in meal duration. Because the pig in our model could not increase its meal duration, it increased its meal frequency instead of its meal size. Model results were difficult to validate with other studies as most studies observed feeding patterns of pigs for a limited BW range and in group-housed conditions (e.g. Hyun et al., 1997), or reported an average value for feeding patterns during the growing period (e.g. De Haer & Merks, 1992). Furthermore, comparison with other studies was limited due to different methods for defining meal criteria and reporting feeding patterns, for instance in feeding bouts or visits (Maselyne et al., 2015). In accordance with Bigelow and Houpt (1988), studies on feeding patterns in pigs showed in general an increase in feed intake, meal size and feeding rate, and a decrease or varying trend in meal frequency, meal duration, and feeding time when pigs gained weight (e.g. Fàbrega et al., 2003; Hyun et al., 1997; Nienaber et al., 1990; Walker, 1991).

To be able to reproduce feeding patterns for validation, it was important to have a similar feeding rate in our model to what was observed in the empirical study of Bigelow and Houpt (1988). The feeding rate equation in our model produced a linear increase of feeding rate, similar to empirical studies (e.g. Hyun et al., 1997; Rauw et al., 2006). The feeding rate in the study of Bigelow and Houpt (1988), however, was not increasing linearly, especially after pigs reaching approximately 80 kg of BW. An explanation for the change in feeding rate is not given in that study, but it could be related to conditions in the study such as the reported variations in water intake or the required panel pressing to obtain feed. The effect of feeding rate on other feeding patterns in the model showed similar inter-relatedness of feeding patterns as reviewed by Nielsen (1999): when meal frequency, meal size and meal duration are

known, daily feed intake, daily feeding time and feeding rate can be derived from these parameters. Although feeding rate affected most feeding patterns, it did not affect daily feed intake as pigs adapted their feeding patterns to reach the same feed intake level. For future research, it would be interesting to study the development of feeding rate for group-housed pigs in the model. Changes in feeding rate of group-housed pigs are not fully understood and could be an interesting indicator for social pressure (Nielsen, 1999).

Feeding rate, meal duration or other feeding patterns did not affect feed intake and BW gain. There, however, was a small deviation in BW gain of pigs when using the feeding rate values of Bigelow and Houpt (1988) at the end of the simulations. Due to the reduced feeding rate, pigs needed to increase their feeding time to reach the same daily feed intake as with a higher feeding rate. This increase in feeding time resulted in more energy use per day, and consequently a slightly decreased BW gain. The sensitivity analysis showed that *Diet\_palatability* was the parameter affecting meal size, feed intake and BW gain most. The effect of *Diet\_palatability* on feed intake corresponds to empirical results. Several studies in humans showed the effect of increased food intake and larger meal sizes with more palatable food (see for review Sørensen et al., 2003). Studies in pigs showed increased feed intake and daily BW gain with preferred diets (e.g. Janz et al., 2007). Besides *Diet\_palatability*, *Response\_to\_light* also affected feed intake and BW gain. This could indicate that light intensity can affect feeding behaviour. There is no indication in literature, however, that feed intake and BW gain in pigs are affected by the intensity of light (e.g. Wheelhouse & Hacker, 1982). A more likely explanation is that response to light is an individual pig trait. Individual differences among pigs were shown, for example, in melatonin response to darkness (Tast et al., 2001a). Melatonin response is related to the sleep-wakefulness cycle, which follows the same diurnal rhythm as feeding behaviour, and in which sleeping and active behaviours alternate (Reilly & Waterhouse, 2007). A large individual variation in response to light, however, is not expected, as different light intensities did not affect melatonin response in pigs above a minimum level of 40 lx light intensity (Tast et al., 2001a).

Due to the modelled conditions of ad libitum feed access and no social competition, we assumed that behavioural decision-making was not affected by emotions. This might be partly besides the truth as studies showed that social isolation can be stressful for individually housed pigs (e.g. Herskin & Jensen, 2000; Ruis et al., 2001) and can affect feeding motivation (Pedersen et al., 2002). Where Nielsen (1999) suggested that pigs in a barren environment without social contact can over-consume feed, Pedersen et al. (2002) showed that pigs valued food more in the company of another pig. These effects were considered secondary in our current model and not expected to change feeding patterns considerably.

This study was the first step in understanding feeding behaviour in pigs. The model presented here showed that combining growth and motivation can explain the changes in the feeding patterns of an individually housed growing pig over time, mostly representing internal factors. Growing pigs, however, are usually housed in groups. Group-housed pigs are known to exhibit different feeding patterns than individually housed pigs, as they feed with a higher feeding rate and have larger, but less frequent, meals (De Haer & Merks, 1992). In addition, group-housed pigs showed a lower feed intake (De Haer & Merks, 1992) and productivity level (De Haer & de Vries, 1993b; Gonyou et al., 1992) compared with individually housed pigs. These differences in feeding behaviour and productivity can be due to social factors, such as social facilitation, competition and stress (Bornett et al., 2000a). Additionally, individual differences in the alteration of feeding patterns were observed among group-housed pigs that were not understood (Bornett et al., 2000a). The current model serves as a basis to include these individual differences and social factors, and to explore the role of social interaction in the causation of feeding patterns in group-housed pigs.

### **3.5 Conclusion**

This modelling study provided insight in how growth and motivation explain the development of feeding patterns of an individually housed pig over time. Pig and feed characteristics affected the motivation to reach a desired level of daily feed intake. Without feeding restrictions, pigs adapted feeding patterns to reach this daily feed intake without affecting feed intake and growth. The use of agent-based modelling for understanding pig behaviour is a novel and promising approach. The developed model is suitable to further study mechanisms underlying feeding behaviour and performance of group-housed pigs.

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## Appendix A. Technical details

### A.1. Details of the sub-model 'Motivational decision-making'

An animal is motivated to feed if its feeding drive ( $F\_drive_m$ ) is higher than its satiation ( $F\_satiation_m$ ) expressed per minute.  $F\_drive_m$  is a function based on the energy balance of the animal ( $E\_balance_d$ ) each minute, palatability of the feed ( $Diet\_palatability$ ) and the diurnal rhythm ( $D\_rhythm$ ) (Sauvant et al., 1996). For pigs it is known that the nutrient balance can affect feeding behaviour (NRC, 2012) and, therefore, the nutrient balance ( $N\_balance$ ) was also added to Equation 1. As the pig in the model received ad libitum feed that met its nutritional requirements, it is assumed that  $N\_balance$  had no effect on  $F\_drive_m$ . In that case, the value for  $N\_balance$  was set to 1.0.

$$(1) \quad F\_drive_m = E\_balance_d \times Diet\_palatability \times D\_rhythm \times N\_balance$$

For  $Diet\_palatability$  a fixed dimensionless value (0.85) was used because it was assumed that feed is always available with the same potential palatability. The value 0.85 was chosen after calibration of the model on expected amount of feed intake.  $D\_rhythm$  was represented by two dimensionless values: a higher value for the response to light ( $Response\_to\_light$ ) from 08:00 to 19:00 hour (0.7) and a lower value for the response to darkness ( $Response\_to\_darkness$ ) from 19:00 to 08:00 hour (0.5). The values 0.7 and 0.5 were chosen after calibration of the model on expected distribution of feed intake over a 24 h period.  $E\_balance_d$  was included in the model as a coefficient equal to 1 if the digestible energy (DE) absorption (kJ DE) of a pig that day ( $E\_absorption_d$ ) was high enough to meet the energy requirements (kJ DE) of that day ( $E\_requirement_d$ ). If the energy requirements were not met, the coefficient was higher than 1 and increased the feeding drive.  $E\_balance_d$  was calculated analogously to the model of Sauvant et al. (1996).

$$(2) \quad E\_balance_d = Maximum \left( \frac{E\_requirement_d}{E\_absorption_d}, 1 \right)$$

The equation for  $E\_absorption_d$  was adjusted to make a better fit to a situation of an intensively, individually housed pig and the parameters in this model.  $E\_absorption_d$  (kJ DE) was calculated as the sum of absorbed energy ( $E\_absorption_m$ ), based on passed minutes that day ( $m$ ) with a maximum of 1440.

$$(3) \quad E\_absorption_d = \sum_{m=1}^m E\_absorption_m$$

$E_{absorption_m}$  (kJ DE) was the amount of energy that was absorbed in the gut each minute based on digested feed ( $F_{digested_m}$ ) and the energy content of the diet ( $Diet\_DE$ , kJ DE/g).

$$(4) \quad E_{absorption_m} = F_{digested_m} \times Diet\_DE$$

$F_{digested_m}$  (g) was the amount of feed that was digested in the gut each minute based on the gut content ( $Gut\_content_m$ ) and duration of digestion ( $Diet\_digestion$ ).

$$(5) \quad F_{digested_m} = Gut\_content_m \times 1000 \times \frac{1}{Diet\_digestion}$$

In a study of Lewis and McGlone (2008) on pigs with ad libitum feed, the duration of digestion was on average 20.5 (+/- 0.31) h, with a range of 18 to 24 h. Therefore, it was assumed in the model that  $Diet\_digestion$  was 20.5 hours (1230 minutes).

$E_{requirement_d}$  (kJ DE) was based on energy use for maintenance and activity and growth capacity since the start of that day. Total energy use was calculated as the sum (with a maximum of 1440 min) of maintenance ( $E_{maintenance_m}$ , Equation 16) and activity ( $E_{activity_m}$ , Equation 19) during passed minutes that day. The potential growth capacity for that day ( $G\_capacity_d$ ) was also based on passed minutes that day.

$$(6) \quad E_{requirement_d} = \sum_{m=1}^m E_{maintenance_m} + \sum_{m=1}^m E_{activity_m} + \left( \frac{G\_capacity_d}{1440} \times m \right)$$

$G\_capacity_d$  (kJ DE) was based on the default daily DE intake of pigs ( $E_{intake_d}$ ) reduced by the sum of energy costs of the previous day for body maintenance ( $PrevE\_maintenance_d$ ) and activity ( $PrevE\_activity_d$ ). At the start of the model, the initial sum of energy costs for  $PrevE\_maintenance_d$  and  $PrevE\_activity_d$  is set to 5800, estimated for a pig with 26.5 kg BW and 18% of the time activity costs.

$$(7) \quad G\_capacity_d = E_{intake_d} - PrevE\_maintenance_d - PrevE\_activity_d$$

$E_{intake_d}$  (kJ DE) was calculated from sex specific equations as described in NRC (2012), converted to DE in kJ. Effective diet metabolisable energy (ME) content of growing pigs was converted to DE by multiplying with 1.03 (NRC, 2012), and converted from kcal to kJ by multiplying with 4.187.

$F_{satiation_m}$  was calculated in a similar way as in the model of Sauvant et al. (1996), where it was based on the rumen load and the instantaneous energy balance ( $E_{balance_m}$ ). Rumen load was based on gut load ( $Gut\_load_m$ ).

$$(8) \quad F_{satiation_m} = Gut\_load_m \times \exp^{(0.1 \times E_{balance_m})}$$



$E\_balance_m$  was calculated based on  $E\_absorption_m$  and the instantaneous requirement of energy ( $E\_requirement_m$ ) per minute.

$$(9) \quad E\_balance_m = \frac{E\_absorption_m - E\_requirement_m}{E\_requirement_m}$$

With  $E\_requirement_m$  (kJ DE) based on the daily energy requirements per day.

$$(10) \quad E\_requirement_m = \frac{E\_intake_d}{1440}$$

$Gut\_load_m$  was a function calculated each minute and based on gut size ( $Gut\_size_m$ ) and  $Gut\_content_m$ , following the equation for rumen load proposed by Sauvant et al. (1996).

$$(11) \quad Gut\_load_m = \exp \frac{Gut\_content_m - Gut\_size_m}{Gut\_size_m}$$

$Gut\_size_m$  (kg) was calculated each minute based on the equation of NRC (2012) to calculate gut fill estimated from empty body weight ( $EBW_m$ ). In the model of Sauvant et al. (1996), gut content was based on ruminal DM and DM content (also based on the size of the feed particles). Pigs, however, are monogastric animals and have no rumen.  $Gut\_content_m$  (kg) in this study was calculated by reducing the amount of feed in the gut in the previous minute ( $Gut\_content_{m-1}$ , kg) with  $F\_digested_m$  each minute. At start of the model, the initial value of  $Gut\_content_{m-1}$  was set to a random value based on a normal distribution with a mean of  $0.5 \times Gut\_size_m$  and standard deviation of  $0.05 \times Gut\_size_m$ .

$$(12) \quad Gut\_content_m = Gut\_content_{m-1} - \left( \frac{F\_digested_m}{1000} \right)$$

## A.2. Details of feeding rate determination

Feeding rate of pigs is related to mouth capacity (Illius & Gordon, 1987), which depends on the size of the animal (Nielsen, 1999; Nienaber et al., 1990) and increases with age and BW (Rauw et al., 2006). Furthermore, feeding rate is related to feed composition (Brouns et al., 1994, 1997). Wellock et al. (2003) included these effects in an equation to calculate the maximum feeding rate of growing pigs ( $FR\_max$ , g per minute). A value of 2.85 was assumed for a high quality pelleted feed and 3.6 for the water-holding capacity related to that feed (Wellock et al., 2003).

$$(13) \quad FR\_max = \frac{(2.85 \times BW^{1.0})}{3.6}$$

$FR_{max}$  is comparable to feeding rates of pigs housed in groups of 30 in the study of Walker (1991), who investigated the effect of feeder availability on feeding behaviour. Wellock et al. (2003) assumed that the feeding rates of these pigs represented maximum feeding rates, because the increase in group size above 20 pigs (and thus increasing feeder occupation) showed a limited further increase in feeding rate. Feeding rates of pigs around 80 kg of BW housed in groups of 10 were almost halved compared to groups of 30 pigs (Walker, 1991). In addition, feeding rates of individually housed pigs were lower than feeding rates of pigs in groups of 8 (De Haer & Merks, 1992). Nielsen (1999) suggested that pigs have a preferred feeding rate, which can increase due to social effects. Based on the work done by Bigelow and Houpt (1988) and Nienaber et al. (1990), we assumed that observed feeding rates of individually housed and ad libitum fed pigs could represent preferred feeding rates. Therefore, preferred feeding rate ( $FR_{preferred}$ , g per minute) was calculated to fit in the range of these feeding rates.

$$(14) \quad FR_{preferred} = FR_{max} \times BW^{-0.25}$$

Additional factors that can affect feeding rate are feed palatability and the level of satiation (Sauvant et al., 1996). Therefore these factors were included in the equation to calculate the actual feeding rate in g per minute ( $FR_m$ ).

$$(15) \quad FR_m = \frac{FR_{preferred} \times Diet_{palatability}}{F_{satiation_m}}$$

### A.3. Details of the sub-model Growth

In the model of de Lange (1995), energy requirements for maintenance and activity were calculated by one equation as a function of metabolic BW. To include the effect of temperature and variability of animal activity in the model, equations from NRC (2012) were converted to DE in kJ per minute and included in the model to calculate utilisation of energy for maintenance ( $E_{maintenance_m}$ , kJ DE), based on energy use for body maintenance ( $E_{body_m}$ ) and energy use for thermogenesis ( $E_{thermogenesis_m}$ ).

$$(16) \quad E_{maintenance_m} = E_{body_m} + E_{thermogenesis_m}$$

$E_{body_m}$  (kJ DE) was based on  $BW$  (NRC, 2012).

$$(17) \quad E_{body_m} = \frac{(197 \times BW^{0.6})}{1440} \times 1.03 \times 4.187$$

$E_{thermogenesis_m}$  (kJ DE) was based on lower critical temperature ( $LCT$ ), temperature ( $T$ ) and  $E_{body_m}$  (NRC, 2012).

$$(18) \ E_{thermogenesis_m} = 0.07425 \times (LCT - T) \times E_{body_m}$$

When a pig is resting or lying energy use is calculated as maintenance energy costs. When a pig is feeding, drinking, exploring or standing additional energy costs for activity are added. Energy costs for activity per minute ( $E_{activity_m}$ , kJ DE) were based on the equation of Van Milgen et al. (1998) and were dependent on the muscle-mass ( $Muscle_{mass_m}$ ) of the body.

$$(19) \ E_{activity_m} = \frac{21 \times Muscle_{mass}^{0.91}}{60} \times 1.03$$

$Muscle_{mass_m}$  (kg) was based on an estimated percentage of muscle mass in Large White castrated males of 43% of  $EBW_m$  (Van Milgen et al., 1998).

Potential body protein growth was based on protein deposition ( $PD$ ) in a pig. In the model of de Lange (1995),  $PD$  was determined by the lowest value of two factors: protein intake and the fixed value of maximum protein retention of a pig per day. To include specific BW effects on  $PD$ , equations from NRC (2012) were included, which defined  $PD$  (g/day) curves for pigs between 25 and 125 kg BW, based on a mean  $PD$  value ( $PD_{mean}$ ) and a standard sex-specific equation. To convert  $PD$  in g/day to g/minute, the value was divided by 1440.  $BW$  and body composition was based on  $EBW_m$  and gut fill (NRC, 2012).  $EBW_m$  was calculated analogously to NRC (2012) by the sum of whole-body lipid mass, whole-body protein mass, whole-body water mass and whole-body ash mass. Gut fill ( $Gut_{size_m}$ ) is calculated from  $EBW_m$  or initial  $BW$  (NRC, 2012).



# Chapter 4

## **The importance of hormonal circadian rhythms in daily feeding patterns: An illustration with simulated pigs**

Iris J.M.M. Boumans<sup>a</sup>, Imke J.M. de Boera<sup>a</sup>, Gert Jan Hofstede<sup>b</sup>, Susanne E. la Fleur<sup>c</sup>, and Eddie A.M. Bokkers<sup>a</sup>

<sup>a</sup> Animal Production Systems group, Wageningen University, Wageningen, the Netherlands

<sup>b</sup> Information Technology group, Wageningen University, Wageningen, the Netherlands

<sup>c</sup> Department of Endocrinology and Metabolism, Academic Medical Center, Amsterdam, the Netherlands

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## **Abstract**

The interaction between metabolic processes and hormonal circadian rhythms underlying feeding behaviour is not well understood. This study aimed to gain deeper understanding of mechanisms underlying circadian feeding behaviour in animals, with a special focus on pigs, *Sus scrofa*. Pigs show an alternans feeding pattern, with a smaller peak of feed intake shortly after the onset of light and a larger peak before the offset of light. We simulated feeding behaviour of pigs over a 24 h period. The simulation model contains mechanisms that regulate feeding behaviour of animals, including processing of feed in the gastrointestinal tract, fluctuation in energy balance, circadian rhythms of melatonin and cortisol and motivational decision-making. Due to interactions between these processes, feeding patterns (e.g. feed intake, meal frequency, feeding rate) emerge. Emerged feeding patterns and patterns of underlying mechanisms (e.g. energy expenditure) were corresponding to empirical patterns, indicating that our model contains relevant mechanisms. Model results show how circadian rhythms in cortisol and melatonin explain the alternans pattern in pigs and how timing and amplitude of cortisol peaks affects diurnal and nocturnal peaks in feed intake. Furthermore, our results indicate that circadian rhythms of other hormones, such as leptin and ghrelin, are less important in circadian regulation of feeding behaviour than previously thought. These results are relevant for animal species having a similar metabolic and endocrine system, such as humans. Moreover, the modelling approach to understand feeding behaviour can be useful for studies in other animal species.

**Keywords:** alternans pattern; feeding behavior; motivation; circadian rhythm; energy balance; pig; melatonin; cortisol; decision-making; modeling.

## 4.1 Introduction

Regulation of feeding behaviour in animals is known to be controlled by the energy balance (Strubbe & van Dijk, 2002). This control includes processing of feed in the gastrointestinal tract (GIT) and metabolic (hunger and satiation) responses of the body to the energy status. The role of circadian rhythms in the regulation of metabolism has been getting more evident recently (Eckel-Mahan & Sassone-Corsi, 2013; Laposky et al., 2008). The sleep-wake cycle, for example, is an important rhythm, as many physiological and behavioural responses of an animal depend on the state of being awake or asleep (Laposky et al., 2008). In addition, several metabolically-related hormonal responses involved in the regulation of energy balance show circadian rhythms, such as cortisol, ghrelin and leptin (Kumar Jha et al., 2015). So far, however, it is unclear how the regulation of the energy balance interacts with circadian rhythms and how this interaction causes feeding behaviour during the day (Strubbe & van Dijk, 2002), such as feed intake, meal frequency and meal size.

Feeding behaviour of animals is observed in recurring daily patterns. These patterns usually coincide with the active periods of animals and commonly consist of two peaks. A distinction can be made between a bigeminus activity pattern, where the first peak exceeds the second peak, and an alternans activity pattern, where the second peak exceeds the first peak (Aschoff, 1957). The bigeminus pattern is observed, for example, in Greenfinches, *Chloris chloris*, and meadow voles, *Microtus pennsylvanicus* (Aschoff, 1966), whereas the alternans pattern is observed in species such as the Capercaillie, *Tetrao urogallus* (Gjerde & Wegge, 1987), and pigs, *Sus scrofa* (De Haer & Merks, 1992; Schouten, 1986).

For animals with a bigeminus pattern of feed intake, the higher first peak of feed intake can be explained by energy deficits after a period of mainly fasting. Animals with an alternans pattern of feed intake, however, have a higher peak in the second part of the active period, suggesting that other mechanisms besides the energy deficits after fasting regulate their feed intake. Insight in these mechanisms will enhance our understanding of the ability of animals to adjust their feeding behaviour under various conditions and can provide insight in their growth and health.

The aim of this study is to gain more understanding of the mechanisms underlying circadian feeding behaviour in animals. We hypothesise that hormones with strong circadian rhythms involved in the energy balance can explain feeding patterns, in particular in the regulation of the alternans feeding pattern. We focus in this study on pigs, because they have an alternans feeding pattern and a large amount of empirical data is available on, for example, circadian fluctuations in physiological processes and feeding behaviours (e.g. meal frequency, meal size, meal duration).

### **4.1.1 General approach**

We used a computer model to mechanistically simulate the regulation of feeding behaviour. Feeding behaviour is very complex and interactions take place at many levels (e.g. from molecular, cellular, neurological, to whole animal level). We chose to simulate underlying processes on a physiological and metabolic level, integrating processing of feed in the GIT (intake, digestion and absorption), fluctuation in the energy balance, and hormonal circadian rhythms that affect motivational decision-making on behavioural patterns such as feeding behaviour.

The model allowed us to test the effect of interaction between the energy balance and hormonal circadian rhythms on feeding patterns. Feeding patterns such as feed intake, meal frequency and meal duration emerged when running the model. Furthermore, the model produced patterns of underlying processes, such as energy absorption, metabolic rate and daily energy balance. Model patterns were compared to those observed in empirical studies for validation of the model.

## **4.2 Energy balance**

Animals feed in meals and hence energy intake is episodic, while the need for energy is variable but continuous (Nelson, 2011; Stricker & Verbalis, 1988). The energy balance, therefore, will shift continuously between a positive and a negative balance, which is regulated on short and long term.

### **4.2.1 Processing of feed**

In monogastric animals, such as pigs, ingested feed first enters the stomach, which functions as a temporarily storage. From the stomach, digesta is transferred to the intestines where energy is absorbed (Strathe et al., 2008; Wenk, 2001). Woods and D'Alessio (2008) reviewed hormonal and related signals affecting energy intake. Shortly after ingestion, satiation signals from the GIT, such as cholecystokinin (CCK), glucagon-like peptide-1 (GLP-1) and peptide tyrosine-tyrosine (PYY), and distension signals from the stomach are arising (Woods & D'Alessio, 2008). These signals contribute to digestion of feed (e.g. stimulating gut motility and secretions) and are anorexigenic signals that decrease appetite and feed intake. After fasting, orexigenic peptide concentrations of ghrelin increase and stimulate appetite and feed intake.

### **4.2.2 Energy balance**

The energy balance is determined by energy absorption and energy expenditure (see review Schwartz et al., 2003). The balance will shift from positive to negative during the day and affect anabolic and catabolic processes in the body of storing (e.g. fatty acid and protein synthesis) or releasing energy (e.g. glycolysis and fatty acid oxidation). These processes will affect the amount of body fat (adiposity) of the



animal. As reviewed by Woods and D'Alessio (2008), adiposity of the animal affects circulating insulin and leptin levels. The amount of adipose tissue is related to plasma leptin concentrations and a basal amount of plasma insulin is available as a reflection of the amount of fat. While satiation signals from the processing of feed are secreted in phases during meal intake, adiposity signals are more continuously present and affect the energy balance on the long term. These anorexigenic adiposity signals affect anabolic and catabolic processes and change the sensitivity of the brain to satiation signals.

### 4.3 Circadian rhythms

Circadian rhythms that underlie behavioural patterns are regulated by internal body clocks (endogenous oscillators) (Aschoff, 1963, 1966). These body clocks can adjust physiological and behavioural responses of an animal to promote or inhibit feeding behaviour at certain time moments (Strubbe & van Dijk, 2002). Periodic environmental factors, known as *zeitgebers*, synchronize responses of an animal to a 24 h period (Aschoff, 1966). The light-dark cycle is an important *zeitgeber* in these rhythms. Light synchronises the suprachiasmatic nuclei (SCN) in the anterior hypothalamus of the brain (the master clock), which regulates circadian rhythms in the body such as sleep-wake cycle and behavioural activity (Johnston, 2014). Under normal conditions, with ad libitum feed access and a normal light-dark cycle, the master clock synchronises with peripheral oscillators (outside the SCN), to synchronize processes such as fasting and feeding behaviour (Kumar Jha et al., 2015). While the light-dark cycle is an important *zeitgeber* for the circadian clock, feed availability is an important *zeitgeber* for peripheral oscillators involved in the regulation of circadian feeding behaviour (Kriegsfeld et al., 2002).

Some hormones involved in the regulation of energy balance show strong circadian rhythms. In mammals, these hormones include melatonin, leptin, ghrelin, and glucocorticoids (see review Kumar Jha et al., 2015). Melatonin concentrations fluctuate during the day following the light-dark cycle, with secretion mainly at night in both diurnal and nocturnal animals (Claustrat et al., 2005; Kumar Jha et al., 2015). Melatonin causes sleep in diurnal mammals, but not in nocturnal mammals. Nocturnal animals are active when melatonin levels are high during the night (Kumar Jha et al., 2015). Leptin stimulates energy expenditure and inhibits feed intake, while ghrelin has an opposite effect and counterbalances actions of leptin (Kumar Jha et al., 2015). Glucocorticoids are light-entrainable and peak shortly before the onset of activity, which means shortly before light in diurnal animals or shortly before the offset of light in nocturnal animals (Dallman et al., 2004). In addition, glucocorticoids also can be entrained to feed availability when kept under feed-restricted conditions (Dallman et al., 2004). Glucocorticoids are involved in several biological functions, including metabolic mechanisms such as stimulation of gluconeogenesis and fat breakdown by

lipolysis to maintain blood glucose levels (De Guia et al., 2014). Although they also induce anabolic effects, they are generally viewed as catabolic hormones (Peckett et al., 2011).

Since feed availability is an important *zeitgeber* in metabolism, fluctuations in many circulating hormone concentrations are related to feed intake patterns. In a study with pigs that were feed deprived for 72 h, serum concentrations of insulin-like growth factor 1 (IGF-1, a hormone with anabolic effects), leptin, ghrelin and cortisol were collected every 12 h. While the circadian patterns of IGF-1, leptin and ghrelin disappeared, cortisol levels increased but retained in a comparable circadian rhythm (Salfen et al., 2003). This suggests that cortisol rhythms are feed independent and might be important in the causation of an alternans feeding pattern. Besides cortisol, melatonin patterns are also known to be less affected by feed intake (Kriegsfeld et al., 2002). This suggests that melatonin and cortisol might be important in the causation of the circadian feeding pattern under ad libitum feeding conditions. They might function as markers for the body to stimulate the feeding or fasting state, while other hormones might rather be stimulating or inhibiting feeding behaviour as a reaction following the energy status of an animal.

#### **4.3.1 Melatonin in pigs**

Blood melatonin concentrations in pigs can range from <0.3 pg/ml during light to 15 pg/ml during night (Tast et al., 2001b). While some studies showed a circadian rhythm in circulating melatonin in pigs (e.g. Paterson et al., 1992; Tast et al., 2001b), others did not find such a circadian rhythm (e.g. Minton et al., 1989). This might be explained, besides different light effects, by inadequacies in the tests used (Tast et al., 2001b) or by the effect of feed intake, which can increase melatonin levels after a meal (Bubenik et al., 2000). Therefore, Tast et al. (2001b) concluded that pigs most likely show a circadian rhythm with nocturnal peaks in melatonin.

#### **4.3.2 Cortisol in pigs**

Cortisol is a steroid hormone in pigs. Like other diurnal animals, pigs show a circadian pattern with high cortisol levels in the morning (Koopmans et al., 2005; Ruis et al., 1997). In meal fed group housed pigs, for example, plasma corticosteroid concentrations were generally low in the afternoon with about 15 ng/ml and up to 45 ng/ml in the morning (Barnett et al., 1981). Some studies in pigs also show a second cortisol peak in the afternoon (e.g. Hillmann et al., 2008). Besides being light- and feed-entrained, this peak can be induced by stress, which can mask the endogenous rhythm (Kumar Jha et al., 2015).

### 4.3.3 Hypotheses

Based on the literature discussed above we hypothesised that:

- Circadian rhythms in circulating melatonin and cortisol affect the daily energy balance in pigs by stimulating catabolic processes.
- The interaction between the energy balance and circadian rhythms of circulating melatonin and cortisol can explain the alternans feeding pattern in pigs.
- Circadian rhythms observed in other circulating hormones involved in metabolism (e.g. leptin and ghrelin) follow the energy balance caused by the circadian feeding pattern

## 4.4 Model description and methods

The model is developed in Netlogo 5.3 and simulates the feeding behaviour of an individually housed pig. The environment in the model represents conventional housing in a barren pen with a concrete floor and ad libitum access to feed and water. The model builds on a model that was developed in a previous study on feeding patterns of a pig during the entire growing period (Boumans et al., 2015). In both models, feeding behaviour emerges from the interaction of 1) sub-model Motivational decision-making and 2) sub-model Growth, both affected by pig and feed characteristics (Figure 1).

The time step in the model is 1 min, adding up to days of 24 h (1440 min). The sub-model Growth calculates the body weight of a pig each time step, based on energy, protein and amino acids for energy expenditure and remaining energy for storage of protein and lipid in the body (see Boumans et al., 2015 for more detailed information). The sub-model Motivational decision-making is divided into four parts: processing of feed in the GIT, energy balance, circadian rhythms and motivations. These parts were further extended and integrated in the model in this study. The processes in each part are explained below.

**Table 1.** Equations used in processes in the sub-model Motivation decision-making.

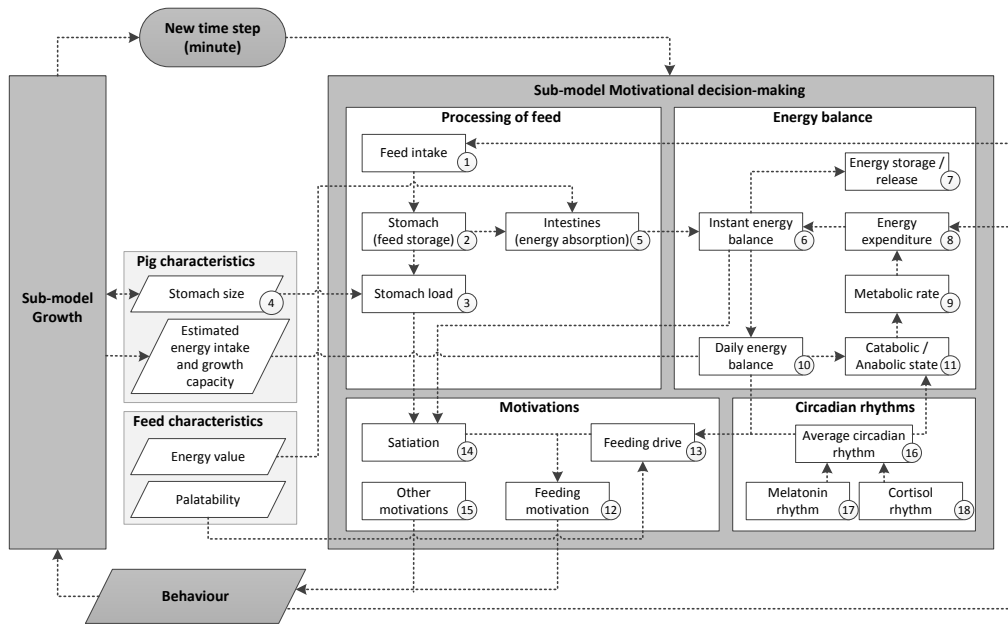
No.	Process	Equation	Reference
<i>Processing of feed</i>			
1	Feeding rate (g/min)	Maximum ((([maximum feeding rate, g/min] x [palatability] / exp ([satiation] * 0.1)), [maximum feeding rate, g/min]) Where: Maximum feeding rate (g/min) = (2.85 x [body weight]) / 3.6	Adapted from Boumans et al. (2015); Young and Lawrence (1994).
2	Stomach passage (g/min)	Sum ([amount of feed at intake, g] x exp (-0.05 x [time in stomach, min]))	Strathe et al. (2008).
3	Stomach load	Exp ((([stomach content, g] / 1000) - [stomach size, kg]) / [stomach size, kg])	Adapted from Boumans et al. (2015).
4	Stomach size (kg)	[Gut size, kg] x 0.3	Adapted from Boumans et al. (2015); Wenk (2001).
5	Energy absorption (kJ/min)	[Intestines content, kg] x 1000 x [passage rate, g/min] x [energy content of the diet, kJ/g]	Adapted from Boumans et al. (2015).
<i>Energy balance</i>			
6	Instant energy balance (kJ/min)	[Energy absorption, kJ/min] - [energy expenditure, kJ/min]	Adapted from Boumans et al. (2015).
7	Energy storage/release (kJ/min)	[Instant energy balance, kJ/min]	Boumans et al. (2015).
8	Energy expenditure (kJ/min)	[Metabolic rate, kJ/min] + [feed digestion, kJ/g/min] + [energy activity, kJ/min]	Adapted from Boumans et al. (2015); Verstegen et al. (1991); Noblet et al. (1993).
9	Metabolic rate (kJ/min)	[Cost maintenance, kJ/min] / exp ([catabolic/anabolic state] - 1 x 0.2) Where: Cost maintenance (kJ/min) = [standard cost maintenance, kJ/min] + [thermogenesis, kJ/min]	Adapted from Boumans et al. (2015); NRC (2012); Schwartz et al. (2003).
10	Daily energy balance	[Estimated daily energy intake, kJ] / ([estimated daily energy intake, kJ] + sum ([instant energy balance, kJ/min] - [estimated growth capacity, kJ]))	Adapted from Boumans et al. (2015); Sauvante et al. (1996); (NRC, 2012).
11	Catabolic/anabolic state	(2 - [Daily energy balance]) x [average circadian rhythm]	Based on Schwartz et al. (2003).
<i>Motivations</i>			
12	Feeding motivation	[Feeding-drive] - [satiation] + [positive feedback]	Boumans et al. (2015).
13	Feeding drive	[Palatability] x [daily energy balance] / [circadian rhythm]	Adapted from Boumans et al. (2015).
14	Satiation	[Stomach load] x exp (0.1 x [instant energy balance, kJ/min])	Boumans et al. (2015).
15	Other motivations (drinking, exploring, lying)	[Drive] - [threshold] Where: Threshold (for drinking & exploring motivation) = [average circadian rhythm] / 6 Threshold (for lying motivation) = 1 - [circadian rhythm melatonin]	Adapted from Boumans et al. (2015).

**Table 1.** Continued

No.	Process	Equation	Reference
<i>Circadian rhythms</i>			
16	Average circadian rhythm	$(((\text{circadian rhythm cortisol}) \times 2) + [\text{circadian rhythm melatonin}]) / 3$	Adapted from Boumans et al. (2015), based on Kumar Jha et al. (2015); Tast et al. (2001b).
17	Circadian rhythm melatonin	From 06:00-18:00 h (light period) = 0.4 From 18:00-06:00 h (dark period) = 0.8	
18	Circadian rhythm cortisol	$1 + 1 \times \sin(((2 \times \pi / 1440) \times ([\text{min}] - 1380)) \times (180 / \pi))$	Based on Ekkel et al. (1997); Kumar Jha et al. (2015).

#### 4.4.1 Processing of feed in the gastrointestinal tract (GIT)

Processing of feed in the model is divided into feed intake, passage of feed through the stomach, stomach load and passage of feed through the intestines (Figure 1).



**Figure 1.** Schematic overview of model processes involved in the regulation of feeding behaviour in pigs, with emphasis on the sub-model Motivational decision-making (adapted from Boumans et al., 2015). Arrows indicate causal relationships in the model and numbers refer to equations in Table 1.

#### **4.4.1.1 Feed intake**

Feed intake is determined by feeding rate (g/min), which is a function of a maximum feeding rate, palatability of the diet (value = 0.7) and satiation (Table 1, No. 1). The equation to calculate feeding rate was based on Boumans et al. (2015) and adapted to correspond with empirical data on 24 h feeding rate patterns. The effect of preferred feeding rate was excluded since this halved the feeding rate compared to empirical data, the effect of satiation was multiplied by 0.1 to prevent too much fluctuation in the feeding rate during the day and a maximum feeding rate value was included, to prevent that the feeding rate exceeded the maximum feeding rate based on physical limitation.

#### **4.4.1.2 Stomach passage**

Degradation and absorption of feed is assumed to be limited in the stomach (Bastianelli et al., 1996) and is, therefore, excluded from the model. The passage of feed from stomach to intestines is mainly affected by the rate of stomach emptying and intestine contractions (see review Black et al., 2009). Gastric emptying and contractions increase when feed intake is present in the stomach or in the small intestines due to a volume and distension effect of the material (Black et al., 2009). The rate of gastric emptying can be calculated as a first-order reaction in which feed flows from the stomach to the small intestine in 0.231 h<sup>-1</sup> half time ( $T_{1/2}$ ) over a period of about 3 h (Strathe et al., 2008). Therefore, feed passage is calculated as a first-order reaction based on the amount of feed at intake per min and on time passed since feed is in the stomach (to a maximum of 180 min) (Table 1, No. 2).

#### **4.4.1.3 Stomach load**

The amount of feed in the stomach affects gastric distension. Gastric distension will signal to the brain and induce satiation (Maljaars et al., 2007). Gastric distension is calculated as stomach load, based on stomach content and stomach size (Table 1, No. 3). The calculation of stomach load is equal to the equation of gut load in the model of Boumans et al. (2015), whereby gut size is replaced by stomach size. The volume of the stomach of a pig is about 30% of the total volume of the GIT (Wenk, 2001). Stomach size (kg), therefore, is determined as 30% of gut size (Table 1, No. 4). Stomach load represents signals in the processing of feed that are known to affect feed intake. These signals mostly include anorectic satiation signals (e.g. CCK, GLP1, PYY) that decrease feed intake, with one known exception of ghrelin, which is orexigenic and increases feed intake (Cummings & Overduin, 2007).

#### 4.4.1.4 Intestines passage and absorption

Energy absorption in the intestines is based on the amount of digested feed multiplied by the energy content of the feed (14.2 kJ DE/g)(Table 1, No. 5). Digested feed (g/min) is modelled as the ratio of mass (sum of intestines content) to passage rate (1/180). Passage rate is based on the first 3 h (180 min) passage time of digesta in the small intestines. Although degradation of digesta and absorption of nutrients differs among parts in the small and large intestines, in the first 3 h intensive degradation of digesta occurs in the small intestine, and nutrients, such as protein, carbohydrates, fat, minerals and vitamins, are absorbed (Strathe et al., 2008; Wenk, 2001). We assumed that a more detailed calculation of nutrient absorption is not necessary for development of the feeding patterns. The content of the intestines decreases with the amount of feed that is digested.

#### 4.4.2 Energy balance

##### 4.4.2.1 Instant energy balance

The instant energy balance is modelled as a balance between absorbed energy and energy expenditure per min (Table 1, No. 6). When energy expenditure is lower than energy absorption, a pig stores energy in its body (growth), while it releases energy when energy expenditure is higher than absorption (Table 1, No. 7). This process represents anabolic and catabolic processes in the body.

Energy expenditure is the sum of energy used for maintenance (metabolic rate), feed digestion and activity each min (Table 1, No. 8). Metabolic rate is based on maintenance costs depending on body weight and thermogenesis as described in NRC (2012) and Boumans et al. (2015). Metabolic rate is affected by anabolic and catabolic processes. Catabolic processes increase the metabolic rate, while anabolic processes decrease the metabolic rate (Schwartz et al., 2003). Therefore, an effect of the catabolic/anabolic state of the pig on the metabolic rate is included to generate a variation with a difference of about 30% between peak times and during the night as observed in Verstegen et al. (1991)(Table 1, No. 9). Feed digestion increases energy expenditure with 0.09 kJ per gram digested feed (assuming a 90% dry matter diet), based on Noblet et al. (1993). Activity (which includes all behaviours except lying behaviour) increases energy expenditure each min based on muscle mass of the pig (Boumans et al., 2015; Van Milgen et al., 1998).

##### 4.4.2.2 Daily energy balance

The daily energy balance in the model represents the effect of circulating signals of insulin and leptin, based on the instant energy balance, the estimated daily energy intake and growth capacity that day (Table 1, No. 10). The instant energy balance per

day is calculated as a sum of the instant energy balance based on passed min that day with a maximum of 1440. The estimated daily energy intake and growth capacity is calculated with equations from NRC (2012) on default metabolisable energy intake in pigs based on their weight and sex, and converted to digestible energy in kJ as described in Boumans et al. (2015). Estimated daily energy intake was added to the model (following Sauvant et al., 1996) to prevent a large difference in the energy balance at the start of the day. Also a maximum of 1 was removed from the original model since we assumed that the daily energy balance can both positively as negatively affect the anabolic/catabolic state. When less energy is absorbed than required (negative energy balance), the value of the daily energy balance is above 1. This represents a decrease in concentrations of leptin and insulin and the anabolic pathway (Schwartz et al., 2003). On the contrary, more energy absorption than required (positive energy balance) causes a daily energy balance value lower than 1. This represents an increase in concentrations of leptin and insulin and the catabolic pathway (Schwartz et al., 2003).

#### **4.4.2.3 Catabolic and anabolic state**

The catabolic/anabolic state of a pig in the model is calculated as a multiplication of the daily energy balance and an average circadian rhythm for circulating melatonin and cortisol (Table 1, No. 11). A value above 1 represents a catabolic state, whereas a value below 1 an anabolic state. A negative daily energy balance decreases the catabolic/anabolic state and thus stimulates the anabolic pathway, while a positive daily energy balance increases the catabolic/anabolic state and thus stimulates the catabolic pathway (Schwartz et al., 2003). The average circadian rhythm increases the catabolic/anabolic state when above 1 and decreases this state when below 1.

#### **4.4.3 Motivations**

Each time step the pig decides to perform one behaviour: feeding, exploring, drinking, standing or lying. Feeding, exploring, drinking and lying have underlying motivations. When none of the motivations is above zero, the pig performs standing behaviour if the last behaviour was active, or remains lying if the last behaviour was lying behaviour. Assuming that motivations can be affected by factors that were not included in the model (e.g. emotions), the motivational levels are randomized using a normal distribution, with the calculated motivation level as mean and a (random chosen) standard deviation of 0.0125.

##### **4.4.3.1 Feeding motivation and behaviour**

A pig is motivated to feed when its feeding drive is higher than its satiation (Table 1, No. 12). When feeding behaviour is performed in the previous min, continuing feeding behaviour is stimulated with positive feedback (reinforcement), which temporarily



increases feeding motivation with 0.05 for that time step. Feeding drive is affected by palatability of the feed, the daily energy balance, and the circadian rhythm (Table 1, No. 13), and satiation is affected by the instant energy balance and the stomach load (Table 1, No. 14).

#### **4.4.3.2 Other motivations and behaviours**

Motivations for exploring, drinking and lying are only included to simulate energy use during the day and therefore modelled less comprehensive than feeding motivation. Each motivation is based on a drive and a threshold (Table 1, No. 15). When the drive is higher than the threshold, the pig is motivated to perform the related behaviour. The threshold values for these motivations, as described by Boumans et al. (2015), are replaced by the values derived from the circadian rhythm of melatonin for lying behaviour and the average circadian rhythm for the other behaviours (Table 1, No. 15). Drives increase each time step that the related behaviour is not performed, and decrease when the behaviour is performed (see Boumans et al. (2015) for values and detailed explanation). An additional effect of feed intake on lying drive was simulated. Sleeping behaviour in pigs is associated with increased melatonin from the GIT after passage of feed (Bubenik et al., 2000). This effect was added to the model by increasing the lying drive with 0.0042 per gram of digested feed, which causes one min lying per 50 gram of digested feed. The value for increase of lying drive was chosen randomly, but in a way that it still could reflect realistic lying patterns of a pig.

#### **4.4.4 Circadian rhythms of melatonin and cortisol**

The circadian rhythms of circulating melatonin and cortisol are merged to create an average circadian rhythm (Table 1, No. 16), assuming light-dark entrained rhythms under ad libitum feed conditions. We calibrated the ratio melatonin to cortisol in this calculation at 1:2. The rhythm of melatonin is modelled with a high value during the dark period (from 18:00 to 06:00 h) and a low value during the light period (from 06:00 to 18:00 h) (Table 1, No. 17). This rhythm is comparable to the diurnal rhythm in Boumans et al. (2015) that increased the feeding drive of a pig during daylight and decreased this during night. Furthermore, this rhythm is based on the average rhythms in mammals as outlined by (Kumar Jha et al., 2015) and observed in pigs (e.g. Tast et al., 2001b). The rhythm of cortisol is modelled by a sine function varying with values from 0 to 2 within a cycle of one day, whereby the peak level is at 05:00 h in the morning shortly before light onset (Table 1, No. 18). This rhythm is based on the average rhythms in mammals with a morning peak as outlined by Kumar Jha et al. (2015) and observed in pigs (e.g. Ekkel et al., 1997). The values for melatonin and the magnitude of the fluctuation of cortisol were selected after calibration of the model to expected feed intake patterns and energy expenditure over a 24 h period.

#### 4.4.5 Model analysis

The explanatory values of circadian rhythms of circulating cortisol and melatonin were analysed in four scenarios (Table 2). Regulation of feeding behaviour was simulated without any circadian rhythm (scenario 1), with one circadian rhythm (scenario 2-3) and with both circadian rhythms (scenario 4). In all scenarios, we simulated 50 runs, each representing one gilt with an initial body weight of 28 kg, with ad libitum access to feed and 12 h light between 06:00 and 18:00 h. Model output for analysis included processes in the regulation of feeding behaviour (Table 1) and variables of feeding behaviour. Output variables on feeding behaviour included feed intake (g/h), meal frequency (No./h), meal size (g/meal/h), meal duration (min/meal/h), feeding rate (g/min/h), meal interval (min/h) and feeding time (min/h). Simulation day 30, which represented a pig of about 50 kg body weight, was chosen for analysis of model results. Model results were compared with empirical data on feeding behaviour of individual and group housed pigs.

**Table 2.** Four scenarios to test the effect of circadian rhythms on feeding patterns in pigs.

Scenario	Regulation energy balance <sup>1</sup>	Circadian rhythm of melatonin	Circadian rhythm of cortisol
1.	+	-	-
2.	+	+	-
3.	+	-	+
4.	+	+	+

<sup>1</sup>Includes processing of feed, fluctuation of the energy balance and motivational decision-making on behaviour.

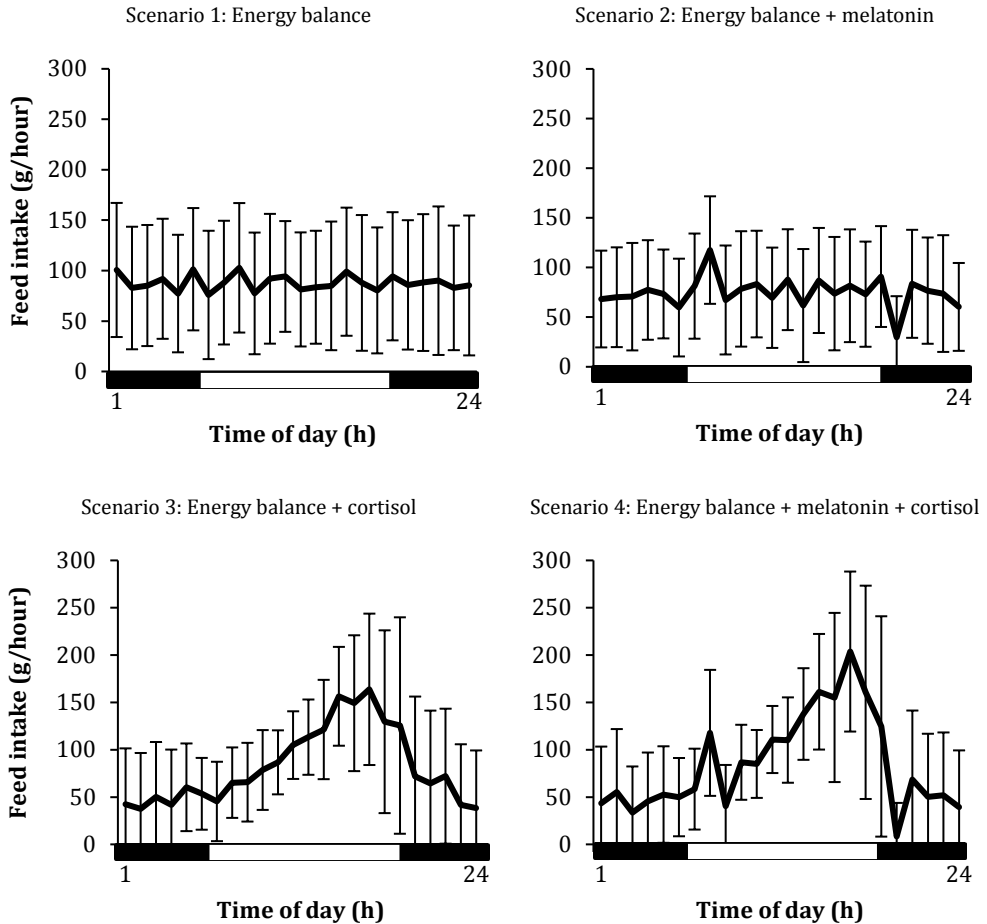
Sensitivity of the feed intake pattern to model parameters was analysed in scenario 4, which is the scenario that corresponds most to empirical patterns. Parameter values of energy level of the diet, palatability of the diet, reinforcement after feeding (positive feedback) and digest duration were varied with 20%. The sensitivity of the feed intake pattern to circadian rhythms was tested by changing amplitude and peak time of melatonin and cortisol rhythms. The contribution of melatonin and cortisol rhythms to the average circadian rhythm was tested by changing the weighing of these rhythms in the average circadian rhythm. Each simulation per parameter change was repeated 50 times.

## 4.5 Results & discussion

### 4.5.1 The effect of circadian rhythms on feed intake in four scenarios

In Figure 2, the result of the four scenarios are presented. In scenario 1, when feeding behaviour was controlled by the metabolic energy balance in absence of any circadian

rhythm, pigs showed a constant 24 h pattern of feed intake fluctuating around an average of 88 gram per h. The circadian melatonin rhythm in scenario 2 caused a peak in feed intake in the morning due to decreased melatonin levels shortly after light, while increased melatonin levels shortly after dark caused a trough followed by a peak in the evening. The circadian cortisol rhythm in scenario 3 caused a feed intake pattern with one peak in the afternoon.



**Figure 2.** Hourly feed intake patterns of pigs in four scenarios. Averages  $\pm$  SD are shown for 50 simulation runs per scenario.

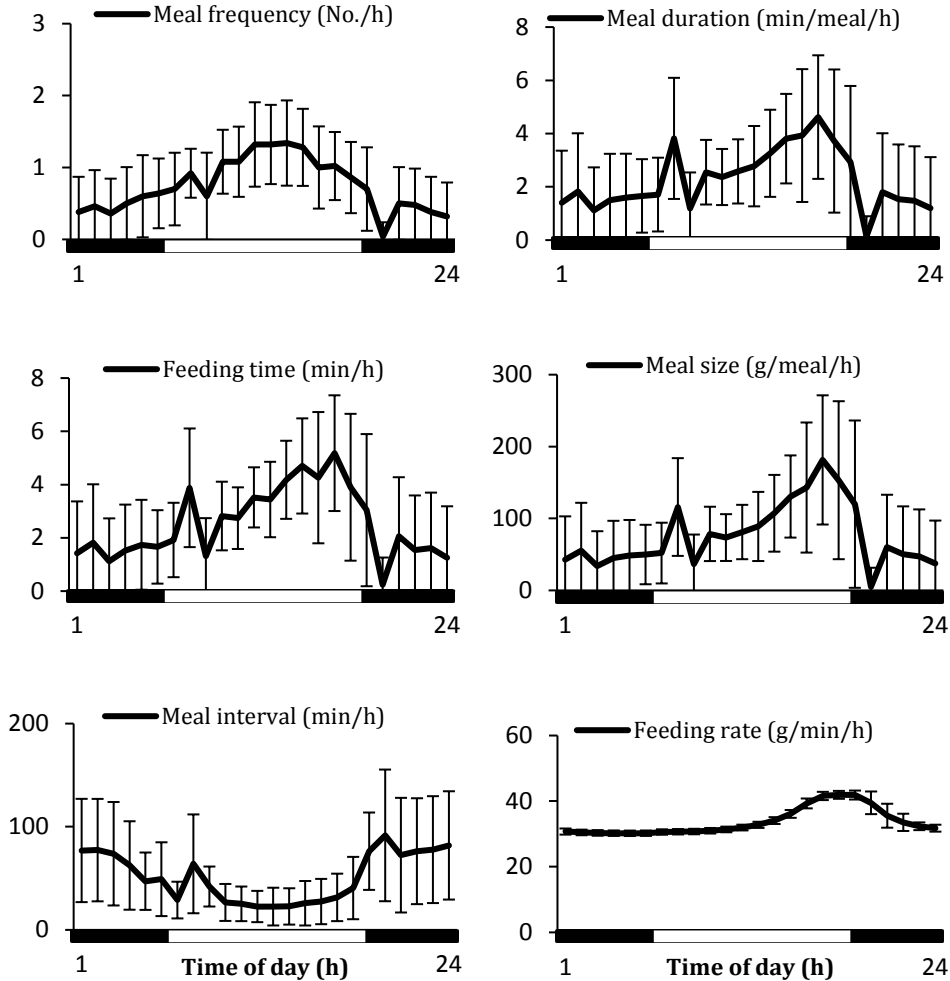
The combined effect of melatonin and cortisol rhythms in scenario 4 caused a feeding pattern resembling an alternans pattern. This pattern includes a low level of feed intake during the night and a high level of feed intake during the day with two peaks: a smaller peak of feed intake shortly after the onset of light and a larger peak before the offset of light. The zero point at 20:00 h and the small peak thereafter is a result of modelling each model run with equal circadian rhythms in cortisol and melatonin. In

real life, however, individual variation in pigs, for example, in melatonin rhythms (Andersson et al., 2000) can cause variation in feeding peaks between pigs, which can smoothen average levels of feed intake as observed in empirical results.

#### **4.5.2 Feeding patterns and patterns of underlying mechanisms in scenario 4**

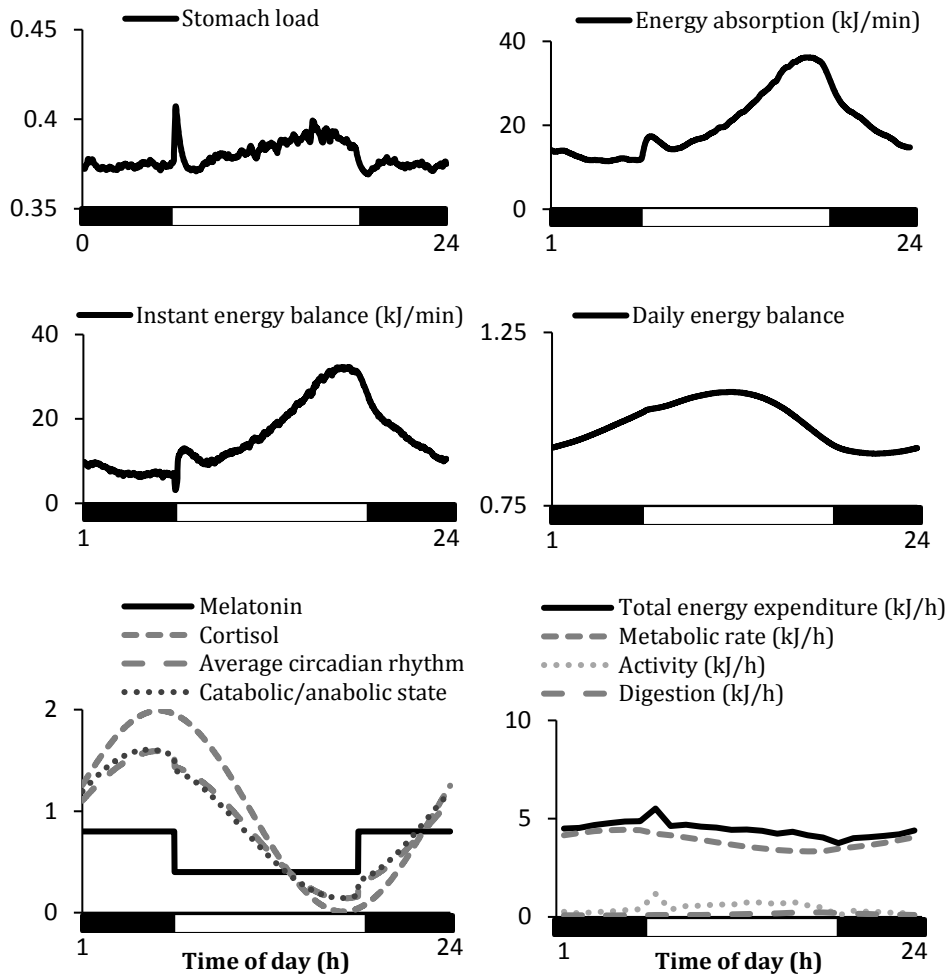
Since the feed intake pattern in scenario 4 corresponded to empirical patterns, we continued with analysing various feeding patterns in scenario 4 (Figure 3). In scenario 4, meal frequency and feeding time showed a similar pattern as feed intake, with two peaks, a small peak around 07:00 h and a larger peak between 11:00 and 16:00 h. This pattern is comparable to the empirical results of De Haer and Merks (1992), who observed a smaller peak around 07:00 h and a larger peak around 15:00 h in both average feed intake (with largest feed intake between 11:00 and 16:00 h) and average feeding time for individually housed pigs (25-100 kg body weight). In their study, the levels of feed intake and feeding time at night (respectively about 50 g/h and 2 min/h) was about a third of the level of the larger peak (respectively about 180 g/h and 6 min/h), which is in line with our results. Bornett et al. (2000a) observed a similar pattern for individually housed pigs (23-86 kg body weight) in meal frequency with on average a small peak (1-3 visits/h) around 9:00 h, a larger peak (3-5 visits/h) around 16:00 h and less than 1 visit/h during the night.

Although the meal frequency we found is lower, the pattern is similar as found by Bornett et al. (2000a). Meal interval was higher during the night than during the day, which can be expected to be opposite to meal frequency. No empirical hourly patterns for meal interval were found, although Schouten (1986) observed a meal interval of on average 100 min during the day and 150 min during the night for crate reared pigs of 14 weeks old. Feeding rate of group housed pigs (30-70 kg body weight) was highest in the afternoon, and lowest in the morning in the study of Young and Lawrence (1994). This is in line with our model results, although the empirical results showed more variation between hours. Meal duration and meal size showed a similar pattern as feed intake. This pattern deviates from the empirical results of Young and Lawrence (1994), who observed peaks in meal size and meal duration around 04:00 and 20:00 h (with respectively 200 g/meal/h and 6.5 min/meal/h). Furthermore, meal size and duration in their study was on average higher during the night than during the day with a trough of about 115 g/meal/h and 3 min/meal/h around 10:00 h. This deviation from empirical results might be caused due to a missing mechanism in the model. For example, one that increases reinforcement of feeding during the night. A deviation in patterns of meal size and duration would be expected to be accompanied by deviations in other feeding patterns, since all feeding patterns are related (e.g. feed intake / meal size = meal frequency). This is not the case, because in contrast to the model patterns of meal size and meal duration, feed intake, feeding time and meal frequency are empirically comparable.



**Figure 3.** Hourly feeding patterns of pigs in scenario 4. Averages  $\pm$  SD are shown for 50 simulation runs.

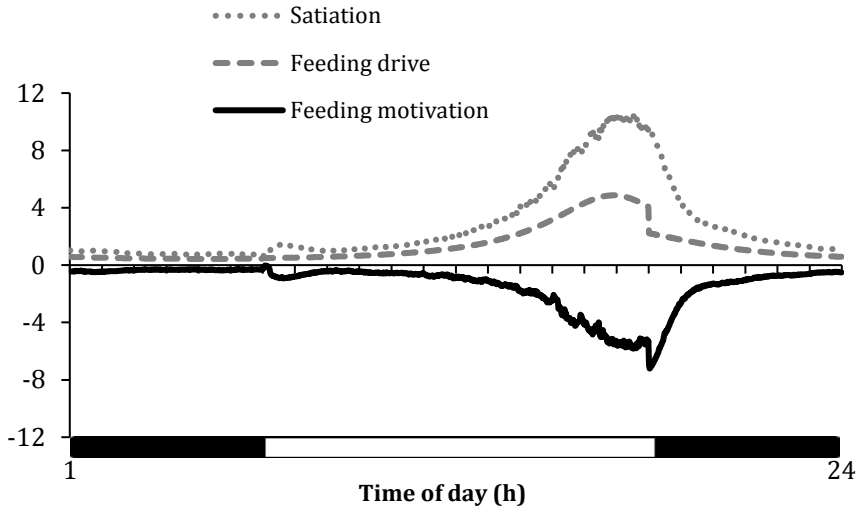
We also analysed patterns of mechanisms underlying feeding behaviour. In Figure 4, the values of variables involved in processing of feed, fluctuation in energy balance and circadian rhythms are shown (see Figure 1 for the position of these variables within model processes). Stomach load, energy absorption and instant energy balance show a short term peak in the morning and a long term peak in the afternoon. While energy absorption and instant energy balance show a higher peak in the afternoon, stomach load shows about equal levels in the morning. The daily energy balance is highest in the middle of the day, indicating a negative energy balance, and lowest in the evening, indicating a positive energy balance. The pattern of the catabolic/anabolic state is similar to the pattern of the average circadian rhythm,



**Figure 4.** Values of variables involved in processing of feed in the gastrointestinal tract, fluctuation in energy balance and circadian rhythms in 24 h. Averages are shown for 50 simulation runs in scenario 4.

which is highest in the morning, inducing a catabolic state and lowest in the afternoon, inducing an anabolic state. Total energy expenditure in our model was a sum of metabolic rate, energy from activity and energy from digestion. As reviewed by Ingram and Dauncey (1985), heat loss (an indication for total energy expenditure) shows a clear circadian rhythm in pigs, with an increase during the day and a decrease during the night. The total energy expenditure in our model, however, showed opposite patterns. This can be a result of energy expenditure from activity in the model, although this pattern seems to be comparable to activity-related heat loss as observed in empirical pigs (Verstegen et al., 1991). Another explanation might be that the energy costs for digestion should have contributed more to the energy

expenditure. Although we based energy costs for digestion on empirical results, it might be that these energy costs were too low compared to the energy costs for the metabolic rate, which we based on results from another empirical study. When we increased the energy costs for digestion, from 0.09 kJ/g to 1 kJ/g digested feed, this indeed resulted in the pattern as described by Ingram and Dauncey (1985), without major effects on feeding patterns (data not shown).



**Figure 5.** Values of variables involved in feeding motivation of pigs in 24 h. Averages are shown for 50 simulation runs in scenario 4.

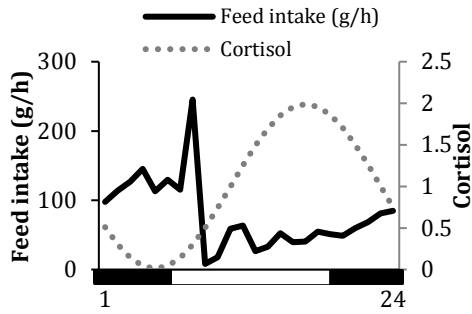
Values of feeding drive and satiation on average approached the same values during the night and were further apart during the day (Figure 5). The feeding drive increased during the day and caused an increased feed intake. Since satiation occurs with a delay, feeding motivation was on average more negative during the day than during the night. Although the rhythm of feeding drive (and satiation) is 5 h earlier in the model, these results are partly comparable to results of an empirical study in humans, which showed a circadian rhythm in hunger with a peak around 20:00 h and trough around 08:00 h (Scheer et al., 2013).

#### 4.5.3 Sensitivity analysis

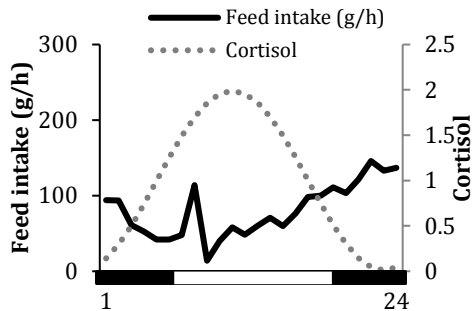
We analysed the sensitivity of the 24 h feed intake pattern with a local sensitivity analysis in which we changed one parameter in the model with 20% increase or decrease. Changing the parameters energy level of the diet, palatability of the diet, reinforcement after feeding (positive feedback) and digest duration had no major impact on the feed intake pattern (data not shown). The model was most sensitive to changes in circulating levels of cortisol and melatonin. A shifted rhythm in cortisol

(peak at 11:00, 17:00 and 23:00 h) caused various feed intake patterns (Figure 6a,b,c). In all scenarios, feeding peaks occurred when cortisol levels were lowest. Peaks during the day caused mainly nocturnal feed intake and peaks during the night caused mainly diurnal feed intake.

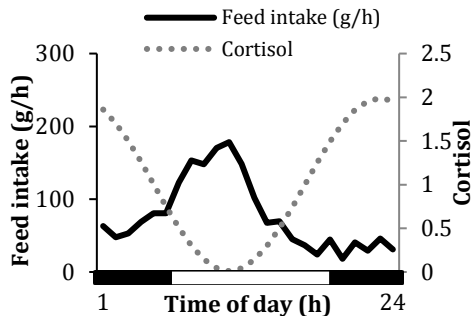
a. Cortisol (peak 17:00 h)



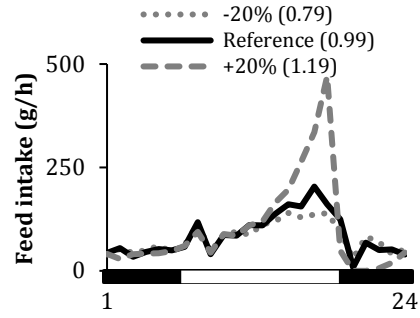
b. Cortisol (peak 11:00 h)



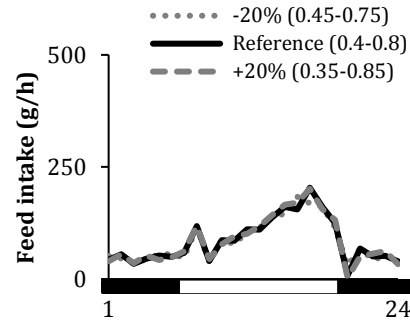
c. Cortisol (peak 23:00 h)



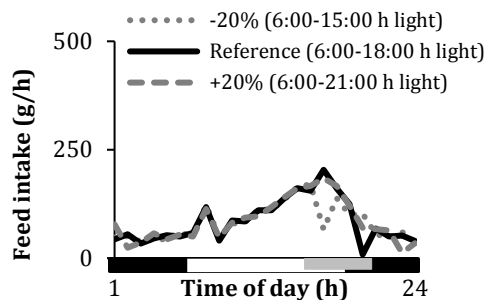
d. Change in cortisol amplitude (peak 05:00 h)



e. Difference in melatonin values during day and night



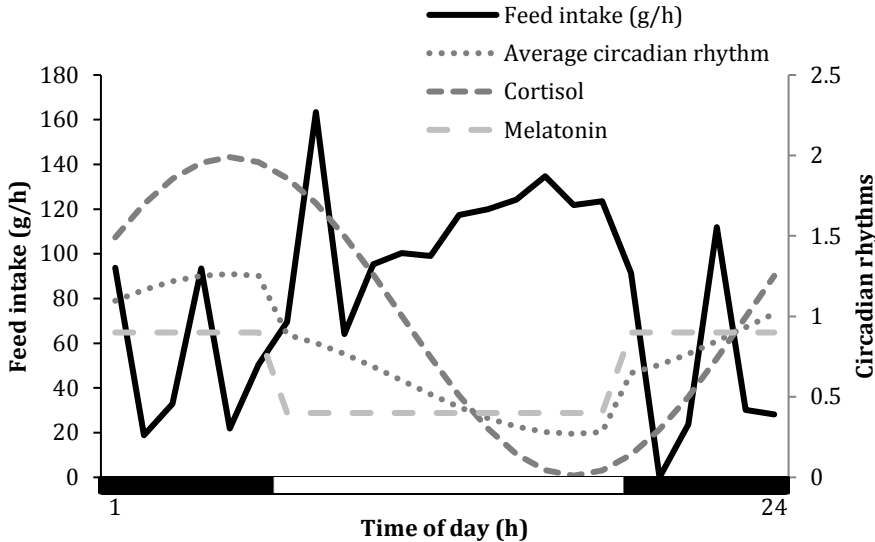
f. Duration of increased/decreased melatonin values



**Figure 6.** Sensitivity analysis of hourly feed intake patterns to variations in melatonin and cortisol rhythms. Sensitivity to a shifted circadian cortisol rhythm (a, b, c), a different amplitude in cortisol (d), a changed difference between melatonin day and night (e), and a changed duration of increased melatonin levels (f). Averages are shown for 50 simulation runs.



Increasing the cortisol amplitude (when simulating a peak at 05:00h) caused a much higher peak of feed intake in the afternoon, while decreasing the amplitude had limited impact (Figure 6d). Increasing the difference between melatonin levels during day and night had limited impact (Figure 6e). Lengthening or shortening of the light period with a low melatonin value affected feed intake patterns after light offset in the evening (Figure 6f).



**Figure 7.** Hourly feed intake pattern of pigs with an increased effect of melatonin on the average circadian rhythm. The average circadian rhythm is calculated as:  $\text{cortisol} + (\text{melatonin} \times 3) / 4$ . Averages are shown for 50 simulation runs.

Increasing the effect of melatonin on the average circadian rhythm increased feed intake peak in the morning (Figure 7). This pattern can be described as a bigeminus pattern. If we would model this for a nocturnal animal, in which we reverse the effects of melatonin and the peak of cortisol, a pattern similar as in Figure 6 would appear, but then in the night. Compared to feeding patterns in nocturnal rats, our pattern shows similarities with a high and quick increase of the first peak, and a quick decrease of the second peak (e.g. Demaria-Pesce & Nicolaïdis, 1998; Rosenwasser et al., 1981). In rats, however, this first feed intake peak seems to be longer in duration (e.g. 3 or 4 h instead of 2 h as simulated) and the second peak shorter (e.g. 3 h instead of 8 h or more) than in our results.

#### 4.6 General discussion

We hypothesised that circadian rhythms in circulating melatonin and cortisol can affect the energy balance and cause the empirically observed alternans feeding pattern in animals. Our model on pigs showed that the energy balance in itself caused

a continuous pattern of feeding. Including one circadian rhythm only, that of melatonin or cortisol, explained one peak but not both peaks. As hypothesised, including both rhythms of melatonin and cortisol indeed seems to explain the diurnal alternans feeding pattern in pigs. Since the circadian rhythms affected the catabolic and anabolic pathways, in particular the metabolic rate and feeding drive, this would imply that circadian rhythms of melatonin and cortisol regulate the rhythm of the anabolic and catabolic state. Although the importance of these specific rhythms in the causation of feeding patterns has not been shown before, both melatonin rhythms (Laposky et al., 2008) and cortisol rhythms (De Guia et al., 2014) are known to have large effects on the energy balance, and are suggested to be involved in major metabolic diseases in humans, such as obesity and diabetes. Additionally, the importance of melatonin and cortisol rhythms in metabolism was shown in a study with humans, where daily variation in melatonin and cortisol amplitudes was associated with the metabolic syndrome disorder (Corbalán-Tutau et al., 2014).

Other hormones with circadian rhythms, such as ghrelin and leptin, are also thought to be important in the regulation of feeding behaviour. They, however, were not needed to simulate the alternans pattern. This suggests that these hormones more likely follow feed intake as stimulated by the rhythms of cortisol and melatonin. Their dependence on feed intake also appears from changes in rhythms of ghrelin and leptin when pigs had prolonged fasting (Salfen et al., 2003). Leptin and ghrelin concentrations might rather be a signal within the regulation of feeding behaviour, such as a signal about the short or long term energy balance. This relation between ghrelin and the energy balance in pigs was suggested also by Scrimgeour et al. (2008).

Emergent model patterns were in line with empirical patterns, which is an indication that our model contains the relevant mechanisms (Grimm & Railsback, 2012). These emergent patterns included patterns of underlying mechanisms (e.g. energy expenditure, feeding drive) as well as output patterns (e.g. feed intake, meal frequency, feeding rate). Model results were sensitive to the strength (amplitude) and timing of cortisol peaks. In all scenarios, feeding peaks occurred when cortisol levels were low. A reversed cortisol rhythm caused a mainly nocturnal feeding pattern, although the pattern also included diurnal peaks. We did not find literature on cortisol rhythms in night active pigs, though it would be likely that pigs with a nocturnal feeding pattern have a shifted cortisol rhythm, similar to nocturnal animals.

Only if the effect (weight) of cortisol on the average circadian rhythm was increased, an alternans feeding pattern emerged. When the weight of melatonin in the average circadian rhythm was increased, a bigeminus pattern emerged. This might suggest that cortisol rhythms are more leading in alternans feeding patterns, whereas melatonin rhythms are more leading in bigeminus patterns. This could explain why alternans patterns are seen only in diurnal animals, while bigeminus patterns are seen

in both diurnal and nocturnal animals (Aschoff, 1957). Since melatonin levels are high when feeding occurs in nocturnal animals, it is more likely that melatonin is more leading and results in a bigeminus feeding pattern. This difference in melatonin and cortisol between alternans and bigeminus animals might also show in concentrations and ratio of melatonin and cortisol circulating in the blood, where the difference in cortisol and melatonin concentrations might then be higher in pigs. Melatonin levels, however, seem similar when comparing pigs with bigeminus animals, such as rats. Daily blood melatonin levels ranged between 5 and 50 pg/ml plasma in rats (Lewy et al., 1980; Ozaki & Lynch, 1976), while it ranged between <1 and 65 pg/ml in pigs (Bubenik et al., 2000; Minton et al., 1989; Paterson et al., 1992; Tast et al., 2001b). Where cortisol is the dominant glucocorticoid in pigs, this is corticosterone in rats. In contrast to the expectation, corticosterone levels were higher in rats (generally ranging between <1 and 472 ng/ml blood in rats (Atkinson & Waddell, 1997)) than cortisol levels in pigs (between 5 and 75 ng/ml (Barnett et al., 1981; Griffith & Minton, 1991; Koopmans et al., 2005; Malmö et al., 1990; Minton et al., 1989)). Although cortisol and corticosterone are assumed to have the same physiological function, for example in mobilizing energy, there are indications that their function differs (Vera et al., 2012), and therefore these hormones might not be comparable in their function. It might also be that other mechanisms are involved, for example, that these species may have different concentrations of modulators in their blood, such as corticosteroid binding globulin. This carrier protein binds to glucocorticoids and affects its biological activity (Bae & Kratzsch, 2015).

Interestingly, melatonin concentrations in pigs are suggested to be affected by feed intake (Bubenik et al., 2000). A large part of the total circulating melatonin in the body of pigs seems to originate from the GIT. These melatonin levels originating from the GIT are associated with feeding and sleeping periods in pigs. This indicates that melatonin concentrations and consequently activity and inactivity periods in pigs are less dependent on the circadian rhythm following the light-dark cycle than on feed availability. This would explain why pigs seem to switch relatively easily from diurnal activity patterns in conventional settings, to nocturnal activity patterns in natural conditions under the influence of predation or temperature (Schrenk, 1981).

In this study we developed a mechanistic model wherein circadian feeding patterns emerge from interactions between physiological and behavioural mechanisms. This modelling method is new in research to understand feeding behaviour in pigs and underlying mechanisms (Boumans et al., 2015). We believe that our modelling approach can be valuable in studies on feeding behaviour of other animal species than pigs as well. Although behavioural patterns and physiological mechanisms can vary among species, there are also similarities. Nutrient requirements, digestive function and post absorptive metabolism, for example, are comparable between humans and pigs (Miller & Ullrey, 1987). Model values and mechanisms can be adjusted to fit to the

characteristics of human physiology and used to gain more insight in (the physiology-driven part of) feeding behaviour in humans.

### **4.7 Conclusion**

This study shows the importance of circadian rhythms of melatonin and cortisol in the alternans feeding pattern of pigs. This pattern can be explained by the hypothesised combination of a circadian rhythm of melatonin and cortisol. While decreased melatonin levels caused the small peak in the morning, the larger peak in the afternoon is caused by decreased cortisol levels. Furthermore, our study suggests that circadian rhythms of other hormones, such as leptin and ghrelin, might rather be a signal within the regulation of feeding behaviour than controlling feeding patterns. The results also indicate that cortisol and melatonin play a role in the causation of a bigeminus feeding pattern. Our study, therefore, is relevant for more, if not all, animal species with comparable metabolic and endocrine systems. Moreover, the modelling approach used in this study can be useful to study feeding behaviour of other animal species.

### **Acknowledgements**

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# Chapter 5

## **How social factors and behavioural strategies affect feeding and social interaction patterns of pigs in an agent-based model**

Iris J.M.M. Boumans<sup>a</sup> , Imke J.M. de Boer<sup>a</sup>, Gert Jan Hofstede<sup>b</sup>, and Eddie A.M. Bokkers<sup>a</sup>

<sup>a</sup> Animal Production Systems group, Wageningen University, Wageningen, the Netherlands

<sup>b</sup> Information Technology group, Wageningen University, Wageningen, the Netherlands

This chapter has been submitted

## **Abstract**

Animals living in groups compete for food resources and face food conflicts. These conflicts are affected by social factors (e.g. competition level and social facilitation) and behavioural strategies (e.g. avoidance and approach). The interaction among social factors and behavioural strategies is poorly understood. This study aimed to deepen our understanding of the complex interaction between social factors and behavioural strategies affecting feeding and social interaction patterns in animals. We focused on group-housed pigs, *Sus scrofa*, which typically face conflicts around the feeder, and of which patterns in various competitive environments (i.e. pig:feeder ratio) have been documented soundly. An agent-based model was developed to explore how interactions among social factors and behavioural strategies can affect various feeding and social interaction patterns differently under competitive situations. Model results show that pig and diet characteristics interact with group size and affect daily feeding patterns (e.g. feed intake and feeding time) and conflicts around the feeder. The level of competition can cause a turning point in feeding and social interaction patterns. Beyond a certain point of competition, meal-based (e.g. meal frequency and size) and interaction patterns (e.g. avoidance and displacements) are determined mainly by behavioural strategies. The average daily feeding time can be used to predict the group size at which this turning point occurs. Under the model's assumptions, social facilitation was relatively unimportant in the causation of behavioural patterns in pigs. To validate our model, simulated patterns were compared with empirical patterns in conventionally housed growing pigs. Similarities between empirical and model patterns support the model results. Our model can be used as a tool in further research for studying the effect of social factors and group dynamics on individual variation in feeding and social interaction patterns in pigs, as well as in other animal species.

**Keywords:** competition; social facilitation; group dynamics; aggression; avoid; approach, feed intake; welfare.



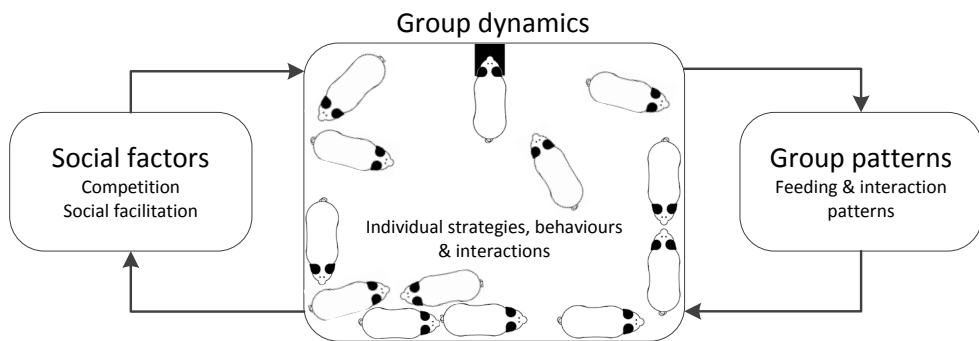
## 5.1 Introduction

Living in groups is associated with competition for food resources. Competition can be low if food is widely available and high if food is scarce or an easily defendable resource. Physiological factors, such as metabolic processes and hormonal circadian rhythms that promote or inhibit food intake in animals, can increase the popularity of certain times for feeding (Strubbe & van Dijk, 2002). This can increase competition for food and the risk of conflicts between animals. Furthermore, social facilitation can stimulate animals to initiate or increase feeding if another animal is feeding (Clayton, 1978), which can further increase the risk of conflicts.

In conflict situations, animals have various behavioural strategies to gain access to food. They can show offensive behaviour and enter (approach) conflicts around food resources or show defensive behaviour to avoid these conflicts. Approaching behaviour includes fights, in which individuals can force others to leave a food resource, whereas avoidance behaviour includes a delay in entering or retreating from a food resource. The decision of an animal to approach or avoid a conflict is affected by various factors, such as the value of the resource, the costs of a fight and the likelihood of winning (Smith & Price, 1973). The physiological state of an animal can affect this decision. A hungry animal, for example, might value a food resource more and has a higher likelihood of winning than a less hungry animal (see review Arnott & Elwood, 2008). Moreover, the probability of a fight can increase when individuals have more equal chances of winning a fight (e.g. small dominance difference) and the benefit of winning is high compared to the cost of losing a fight (Smith & Parker, 1976).

Variation in behavioural strategies of individuals in response to conflicts can lead to different individual feeding and social interaction patterns, such as feeding at desirable or less desirable times, more or fewer (aggressive) interactions, and feeding more or less frequently. The relation between these feeding and social interaction patterns with behavioural strategies and social factors, such as competition and social facilitation, however, is not fully understood. Understanding the mechanisms underlying behavioural patterns is of interest because it can provide insight in the variation of these patterns and the ability of animals to adapt to competitive situations. This is especially relevant for group-living domestic animals, which are not able to leave a group and have to deal with conflicts. These animals are often fed at a single location and at specific times, which can increase competition and defensive behaviour, resulting in high stress and aggression levels (Andersen et al., 2004; Price, 1999). Improved knowledge about competition for food and its effect on behavioural patterns can help in preventing aggression, stress and reduced feed intake in these animals.

Optimizing performance and preventing aggression in farm animals receives much attention in research (e.g. Cornetto et al., 2002; Hemsworth et al., 2013; Szendrő et al., 2015). Empirical studies, however, often show inconsistent results in performance and aggression and it is unclear how social factors and group dynamics affect these results (Estevez et al., 2007). Agent-based modelling can help to increase understanding of potential factors influencing behavioural patterns in animals. This modelling method lends itself particularly well for modelling group dynamics underlying behavioural patterns (Boumans et al., 2016). Agent-based modelling allows to include social interactions, individual variation and time dependent factors. Furthermore, it allows to test the effect of these factors in various combinations and ranges, without the limitation of empirical studies as to costs and use of many animals (Asher et al., 2009).



**Figure 1.** Interactions between social factors, group dynamics and behavioural group patterns in pigs

The aim of this study was to deepen our understanding of the complex interaction between social factors and behavioural strategies affecting feeding and social interaction patterns in animals by using an agent-based model (ABM) (Figure 1). We focus in this study on pigs, *Sus scrofa*. Pigs are a typical example of animals that are housed in fixed group sizes with one feeding place. Group size, and consequently pig:feeder ratio, can reduce accessibility to a feeding place for pigs, and therefore, increase competition and affect feeding behaviour (Nielsen et al., 1996b). An advantage of using domestic animals as subject compared to wild conspecifics, is that they are suggested to have a similar way in behavioural responses and decision-making, while empirical data on their behaviour is better replicable, available in larger sample sizes and less affected by confounding factors such as weather conditions or food resource differences (Andersen et al., 2006).

We carried out a literature study on the development of feeding and interaction behaviour of conventionally housed growing pigs in empirical studies. Based on that study, we developed an ABM that simulates this behaviour under varying pig:feeder

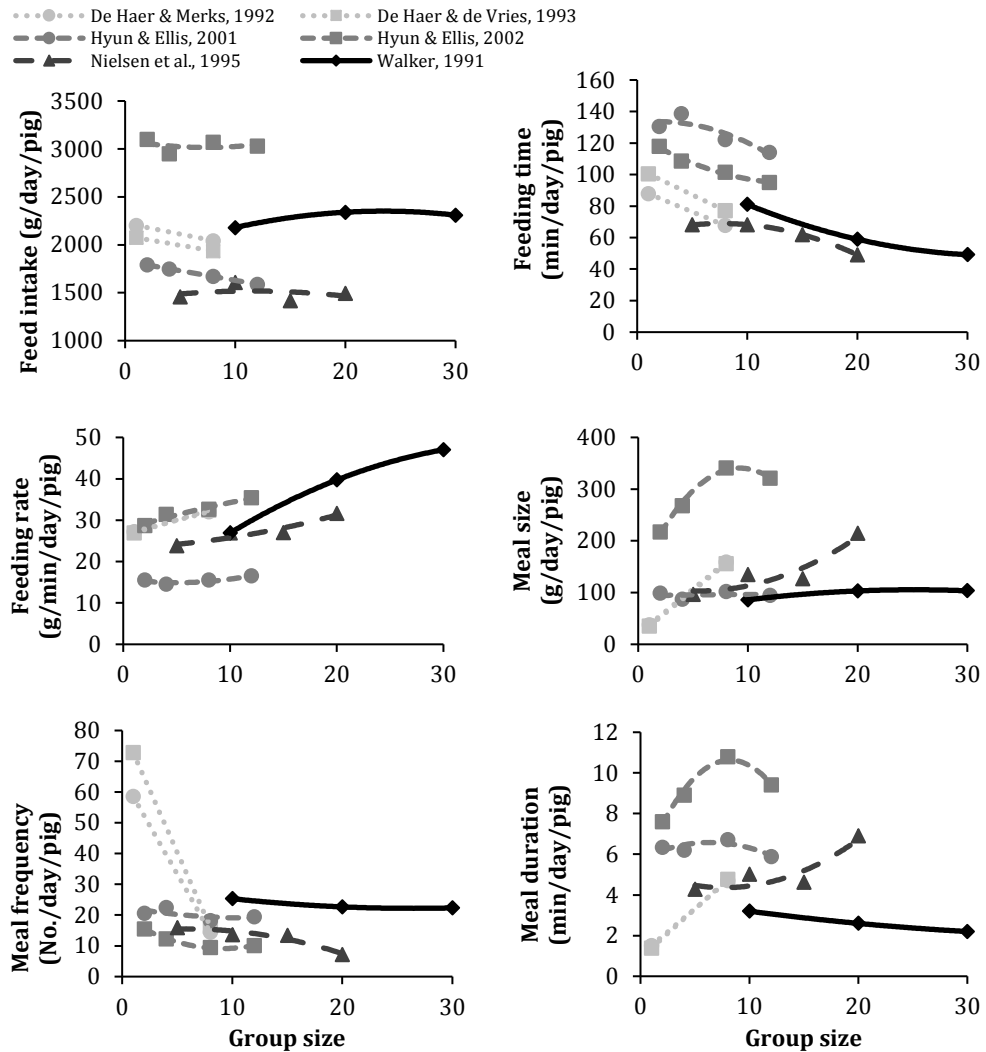
ratios. Pigs (agents) in the model are individually programmed and make behavioural decisions based on their own motivations and interactions with pen mates. The model simulates effects of physiological factors, social factors and behavioural strategies on individual behaviour. This allows exploring the effect of interaction between these aspects on emergent feeding and social interaction patterns of group-housed pigs. In this paper, we first present an overview of empirical feeding and social interaction patterns of pigs in literature and hypothesise about underlying mechanisms. Subsequently, we describe the developed ABM to test these hypotheses, analyse the model results, and discuss the findings.

## **5.2 Empirical feeding & social interaction patterns in pigs**

### **5.2.1 Feeding patterns**

Feeding patterns of growing and finishing pigs with access to one feeding space have been studied in various group sizes (Table 1). Feeding patterns observed in these studies varied (Figure 2), which can be a result of many factors, such as diet characteristics and breed. To avoid having to deal with these various confounding factors, our study focused mainly on the variation in feeding patterns between group sizes within studies, and less on the variation in patterns between studies. Feeding patterns between group sizes show some general trends. Feed intake (g/day) remains relatively similar in all group sizes in the same study. While feeding time (min/day) decreases, feeding rate (g/min) increases with increasing group size. Meal size (g/meal/day) mainly increases in larger groups, whereas meal frequency (no/day) shows exactly an opposite pattern. Meal duration (min/meal/day) shows a pattern similar to meal size, except for the study of Walker (1991), in which meal duration decreases with larger groups.

The meal-based feeding patterns (meal frequency, meal duration and meal size) seem to have a turning point around a group size of 4 to 8 (Hyun & Ellis, 2001), 8 (Hyun & Ellis, 2002) and around 10 to 15 pigs (Nielsen et al., 1995), after which meal patterns change direction (Figure 2). The variation in turning point can be caused by factors, such as space availability and body weight in the specific studies.



**Figure 2.** Feeding patterns of growing and finishing pigs in various group sizes and studies. A polynomial trend line is drawn through data points from empirical studies.

**Table 1.** Characteristics of studies that observed feeding patterns in growing and finishing pigs in various group sizes with one single space feeder and ad libitum access to feed.

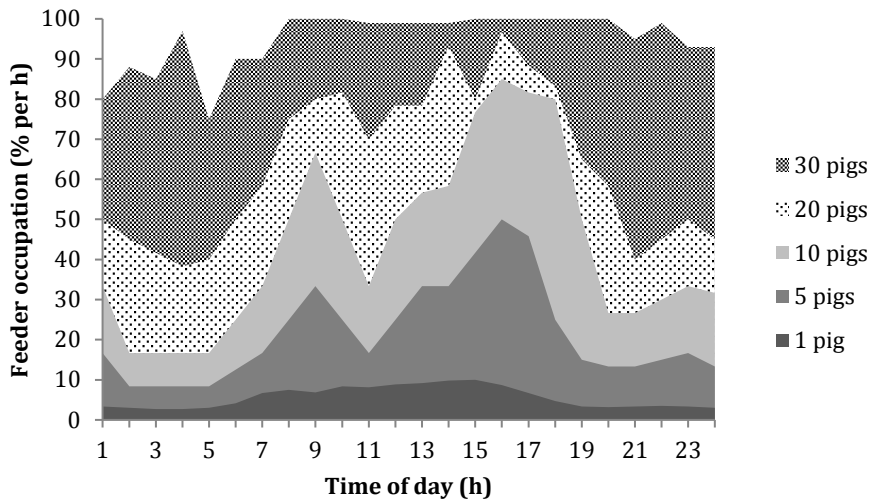
Study	Feeding system	Diet Characteristics	Group size	Body weight range (kg)	Breed	Floor space (m <sup>2</sup> /pig)	Sex
De Haer & Merks, 1992	Electronic feeder (IVOG)	Type unknown, 9.4 - 9.1 MJ NE/kg <sup>1</sup>	1, 8	25-100	Dutch Landrace	3.27 <sup>2</sup> , 0.76 <sup>3</sup>	Males
De Haer & de Vries, 1993	Electronic feeder (IVOG)	Type unknown, 9.4 - 9.1 MJ NE/kg <sup>1</sup>	1, 8	25-100	Dutch Landrace	Unknown	Males and females separated
Hyun & Ellis, 2001	Electronic feeder (FIRE)	Meal-based, 13.8 kJ ME/kg <sup>4</sup>	2, 4, 8, 12	27-48	Crossbred <sup>5</sup>	0.9	Mixed
Hyun & Ellis, 2002	Electronic feeder (FIRE)	Meal-based, 13.9 MJ ME/kg <sup>4</sup>	2, 4, 8, 12	84-113	Crossbred <sup>5</sup>	0.9	Mixed
Nielsen et al., 1995	Electronic feeder (FIRE)	Pellet-based, 13.4 MJ DE/kg <sup>6</sup>	5, 10, 15, 20	34-56	Crossbred <sup>7</sup>	1.06	Males
Walker, 1991	Single space wet & dry feeder	Meal-based, 13.4 MJ DE/kg <sup>6</sup>	10, 20, 30	37-90	Crossbred <sup>7</sup>	0.6	Mixed

<sup>1</sup> Starter and final diet in Netto energy (NE), <sup>2</sup> Individually housed, <sup>3</sup> Group-housed, <sup>4</sup> ME = Metabolisable energy, <sup>5</sup> PIC Line 26 x Camborough 15, <sup>6</sup> DE = Digestible energy, <sup>7</sup> Large White x Landrace

### 5.2.2 Circadian distribution of feeding patterns

In both individually and group housed pigs, feed intake is usually observed in an alternans pattern, with a low level of feed intake during night and two peaks during day, with the highest peak being the second one (e.g. De Haer & Merks, 1992; Nielsen et al., 1995). The distribution of feed intake during day time is more equal in individually housed pigs than in group housed pigs (De Haer & Merks, 1992).

Pigs in small groups occupy the feeder mostly around the peak times, although these peaks merge in the larger groups (Figure 3). In all studies, feeder occupation increases with group size during day and night, although pigs in the largest groups proportionally feed more during night than pigs in the smaller groups (Hyun & Ellis, 2001; Nielsen et al., 1995). Feeder occupation per hour is mostly less than 100%, even during peak times, except for the largest groups (group size 12 and 30 respectively) in the studies of Hyun and Ellis (2001); Walker (1991), which fully occupy the feeder during day time and more than 60% during night time.



**Figure 3.** Distribution of feeder occupation by pigs (% per h) during the day in various group sizes. Based on data from individually housed pig (De Haer & Merks, 1992), group size 5, 10 and 20 (Nielsen et al., 1995), and group size 30 (Walker, 1991).

### 5.2.3 Social interaction patterns around feeding

In group housing, pigs can approach a pen mate at the feeder and (try to) displace it. Nielsen et al. (1995) found that displacements attempts on day 28 increased from 0.37 attempts per pig per h in group size 5 to 1.25 attempts per pig per h in group size 20, whereas the success rate of attempts decreased from 37.9% in size 5 to 7.1% in size 20. Neither the attempts nor the success rates, however, were significantly different. Hyun and Ellis (2001) observed a significantly higher number of forced exits from the feeder in group size 8 (18.8% of observations) and 12 (32.8% of observations) compared to group size 2 and 4 (5% of observations). In addition, Walker (1991) found the average number of pigs queuing (standing or lying and facing the feeder when the feeder was occupied) increased significantly from on average 0.9 pigs in group size 10 to 1.9 pigs in group size 30. Thus, displacements at the feeder seem to occur occasionally, and can occur more frequently in larger groups where the feeder is occupied most of the time.

## 5.3 Hypothesised underlying mechanisms

We hypothesise that interaction between physiological factors, social factors and behavioural strategies can explain the observed feeding and social interaction patterns in pigs. Our hypothesis is further explained below.

### **5.3.1 Physiological factors**

Physiological factors, such as metabolic processes and hormonal circadian rhythms, affect feeding motivation during the day. These factors explain the typical feeding patterns with a low level of feed intake during night and two peaks during day in individually housed pigs (Boumans et al., 2017b). We hypothesise that increased feeding motivation due to circadian rhythms in physiological factors increases competition at specific times among group-housed pigs. Furthermore, feeding motivation might affect the decision for a behavioural strategy of an individual.

### **5.3.2 Social factors and behavioural strategies**

Social facilitation and competition are expected to affect the probability of interactions between pigs and the initiation and termination of feeding behaviour. Social facilitation can increase the probability that pigs want to feed simultaneously and increase competition. The effect of competition on behaviour depends on the behavioural strategy of an individual towards a conflict. Pigs can avoid aggressive behaviour, for example, by waiting to feed till the feeder is free, which can be at less desirable times (Botermans et al., 2000). Avoidance behaviour can explain, for example, why pigs feed proportionally more at night in larger groups (e.g. Hyun & Ellis, 2001; Hyun & Ellis, 2002; Nielsen et al., 1995), even though feeders are rarely fully occupied during assumedly more desired peak times. Avoidance behaviour will prevent interactions and can delay feeding initiation, whereas approaching will cause interactions and can accelerate feeding termination if a feeding pig is displaced from the feeder or delay feeding initiation if the displacement attempt was unsuccessful. Thus competition can explain increased interactions, a decrease in meal frequency by avoidance and unsuccessful approaching behaviour, and a decrease in meal duration by successful approaching and displacement behaviour.

We hypothesise that in response to more competition in larger groups, an increase in the incidence of avoidance strategies explains the empirically observed increase in meal duration and decrease in meal frequency in pigs, whereas an increase in the incidence of approach strategies explains opposite patterns. This would explain why meal-based feeding patterns can change direction from a certain group size onwards. Because feeding patterns are interrelated (Nielsen, 1999), a change in meal frequency or meal duration will also affect the other feeding patterns. When meal frequency decreases, for example, meal size needs to increase to reach the same amount of daily feed intake.

## **5.4 Model description**

A two dimensional ABM was constructed and implemented in the program Netlogo (Wilensky, 1999), version 5.3.0. The model simulates social interactions and feeding

behaviour of individually and group-housed pigs. The model was built in three steps. In the first step, daily feeding patterns of an individually housed pig during the entire growing/fattening period were modelled based on metabolic factors (processing of feed and energy balance) and growth factors (energy use for maintenance, activity and protein and fat deposition) (see Boumans et al., 2015 for detailed explanation). In the second step, hormonal circadian rhythms were included to model feeding patterns within a day (24 h) (Boumans et al., 2017b). In that model, feeding patterns of an individually housed pig emerged per minute affected by internal physiological factors, such as energy absorption, use and requirement (see Boumans et al., 2017b for detailed explanation). The present paper presents the third step in which multiple pigs and social factors were included in the model. While the previous model explained how internal factors motivate a pig to feed, the current model shows how the social context affects feeding and social interaction patterns. The model and a detailed model description following the ODD (Overview, Design concepts, Detail) protocol (Grimm et al., 2006; Grimm et al., 2010) and can be downloaded from the model library on the OpenABM website (<http://www.openabm.org>).

#### **5.4.1 Model environment and agents**

The simulation environment represents a conventional pig housing with a barren pen containing a concrete floor. The housing provides ad libitum access to water, via one watering point, and to feed, via one feeding place, containing a commercial diet that meets the requirements of a growing pig. The feeding place is an assigned area that allows one pig to feed at any time. Other behaviours (exploring, drinking, standing and lying) can be performed simultaneously by multiple pigs

The agents represent growing pigs with individual characteristics such as sex (female, male or castrated male), body weight, growth potential and dominance level. In the standard setting of the model, pigs represent females and start with an body weight of 28 kg. Growth potential of pigs depends on the mean body protein deposition and sex-related growth curve (see Boumans et al., 2015 for detailed explanation). Due to randomisation of potential body protein deposition (based on a normal distribution with the mean corresponding to the mean body protein deposition and a 10% standard deviation) and emerging behavioural patterns and energy use, body weight can diverge among pigs in a pen. At set up of each simulation, pigs are randomly assigned a fixed dominance value that represents their hierarchical position in the group assuming a linear hierarchy. Lower dominance values represent a lower hierarchical position, such that the pig with value one is lowest in rank, followed by two, three, etc.



One time step in the model represents one minute, so that 1440 minutes represent one day. Minutes are associated with time of the day and light and dark periods. Simulations can run to represent the whole growing period of a pig (of about 120 days).

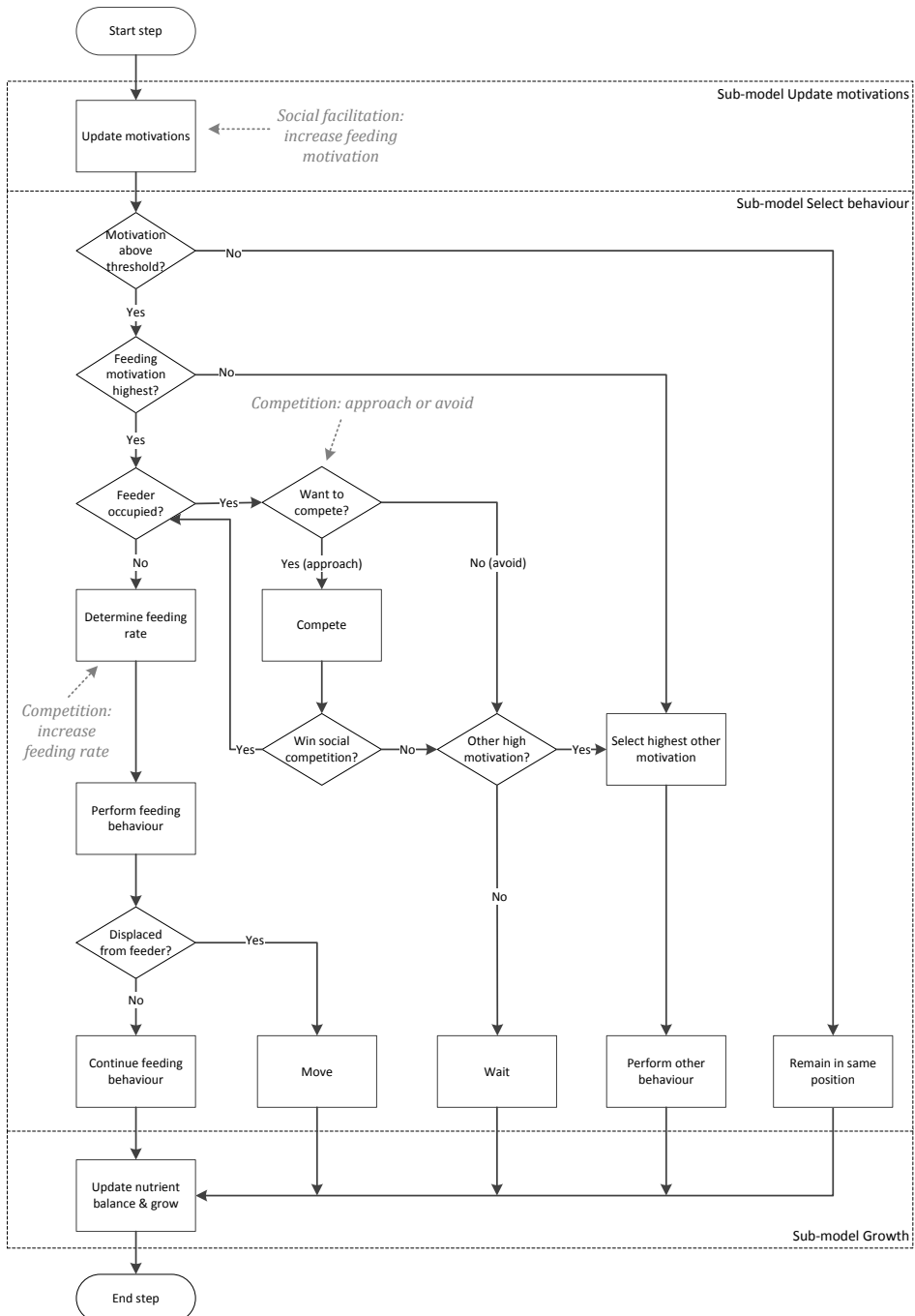
### 5.4.2 Model processes

The decision-making process of a pig per time step consists of three parts: “Update motivations”, “Select behaviour” and “Update nutrient balance & grow” (Figure 4). The included mechanisms are further explained below.

#### 5.4.2.1 Update motivations

Agents update their motivations for feeding, exploring, drinking or lying behaviour each minute. Each motivation is based on a drive and a threshold. The drive represents an internal build-up of energy to perform a certain behaviour, the threshold limits this performance till a required level of drive is gained. When the drive surpasses the threshold, the motivation becomes positive so that the animal is motivated to perform the related behaviour. Drives for exploring, drinking and lying decrease each time step that the related behaviour is performed and increase when the behaviour is not performed (see Boumans et al. (2015) for values and detailed explanation). The threshold for these behaviours is based on circadian rhythms during the day. The threshold for lying, for example, is lower during night time and based on melatonin levels, while at that time the threshold for exploring and drinking is higher based on a combination of melatonin and cortisol levels (see Boumans et al., 2017b for values and detailed explanation).

While motivation for exploring, drinking and lying contains is simulated relatively basic, feeding motivation is simulated more comprehensively, based on metabolic and hormonal processes. A pig is motivated to feed when its *Feeding drive* is higher than its *Satiation*. *Feeding drive* is affected by *Palatability* of the diet, *Daily energy balance* and the *Average circadian rhythm*. *Satiation* is affected by *Stomach load* and *Instant energy balance*. When feeding behaviour is performed in the previous minute, *Positive feedback* (a reinforcement effect) temporarily increases *Feeding motivation* with a fixed value (0.05). For a more detailed explanation about the underlying processes in the model see Boumans et al. (2017b).



**Figure 4.** Flowchart of decisions of an agent each time step. The decision-making process consists of three sub-models (surrounded with dotted lines). Social factors are indicated in grey, with text in italics and dotted arrows. All agents (in random order) go through processes in a sub-model, before continuing to the following sub-model.

### *Social facilitation*

Social facilitation seems stronger in the appetitive phase than in the consummatory phase (Keeling & Hurnik, 1996; Pedersen et al., 2002) and, therefore, is included as a stimulus that temporarily increases feeding motivation of pen mates when a pig is feeding (*Social facilitation*). *Social facilitation* is a fixed value of 0.1 that increases feeding motivation of all non-feeding pigs for that time step. The value for this parameter was chosen after calibration of the model to fit empirically observed feeding patterns.

#### **5.4.2.2 Select behaviour**

Pigs can perform one behaviour per minute: feeding, exploring, drinking, standing or lying. They decide their behaviour based on their motivations for feeding, exploring, drinking or lying. If one or more of these motivations is above zero, the pig wants to perform the behaviour related to the highest motivation. If this behaviour concerns exploring, drinking or lying, the behaviour will be performed. If this behaviour concerns feeding, the pig first checks if the feeder is occupied. If the feeder is free the pig will feed. When none of the motivations is above zero, the pig performs standing (if its last behaviour was active) or lying behaviour (if its last behaviour was lying).

#### *Competition (feeder is occupied)*

If a pig is motivated to feed, but the feeder is occupied by another pig, the pig decides if it wants to avoid or approach its feeding opponent. This decision is based on behavioural rules adapted from Hemelrijk (1999, 2000) and includes a cost-benefit analysis and estimating the success probability. The social dominance levels of opponents are assumed to be an important factor in this estimation as higher and lower ranked pigs in empirical studies show different feeding strategies. Higher ranked pigs, for example, displaced other pigs from the feeder more often (Brouns & Edwards, 1994; Hoy et al., 2012). In the model, therefore, a pig ( $i$ ) calculates its *Relative dominance*, based on its own *Dominance* ( $Dominance_i$ ) and the *Dominance* of its opponent ( $Dominance_j$ ) (equation 1). We assumed an established linear social hierarchy and pigs in the model were randomly assigned a dominance value. The *Relative dominance* is below 0.5 for lower ranked pigs, and above 0.5 for higher ranked pigs.

$$(1) \text{ Relative dominance} = \frac{Dominance_i}{Dominance_i + Dominance_j}$$

It is unlikely that *Relative dominance* is the only factor that affects the decision of a pig to avoid or approach an opponent. Lower ranked pigs can displace higher ranked pigs as well (Hoy et al., 2012). We assume that lower ranked pigs will try to avoid direct competition with higher ranked pigs, but might decide to approach them when their

feeding motivation is high. A food resource can have an increased value for a hungry individual (see review Arnott & Elwood, 2008), therefore, we assumed that *Feeding motivation* increases the value of food and thus the belief that an interaction might be beneficial (*Benefit belief*) (equation 2). The value of feeding motivation is in this case always above zero and might increase to values such as six when pigs cannot feed for longer time. We included an exponential function with the assumption that hungrier animals are more likely to take a risk and reduced the effect with 0.05. The equation was calibrated to allow *Benefit belief* to be slightly higher than the *Relative dominance* (e.g. a pig with a *Relative dominance* of 0.5 and *Feeding motivation* of 1 would have a *Benefit belief* of 0.53, whereas with a *Feeding motivation* of 6 this would be 0.67).

$$(2) \text{ Benefit belief} = \text{Relative dominance} \times \exp^{(\text{Feeding motivation} \times 0.05)}$$

A pig chooses the approach strategy if the value for *Benefit belief* minus *Compete threshold* (a fixed value of 0.2) is greater than the value randomly drawn (RND) between zero and one (equation 3). The value for *Compete threshold* was chosen after calibration to fit the number of interactions to empirically observed interactions. This threshold represents a likely factor such as personality or coping style, in which a pig might be more or less reluctant to initiate an interaction. High resistant and more aggressive pigs, for example, are more likely to initiate a fight independent of their likeliness to win (Bolhuis et al., 2005a; Camerlink et al., 2015). A pig that chooses the approach strategy will compete with its opponent and attempt to displace the opponent pig from the feeder. The alternative is to avoid an opponent and to perform another behaviour (Figure 4). This behaviour is related to the second highest motivated behaviour or, if no other motivation is above zero, waiting behaviour.

$$(3) \text{ Approach strategy} = \text{Benefit belief} - \text{Compete threshold} > \text{RND} (0,1)$$

Wins and losses resulting from an approach strategy are modelled based on the *Success probability* of both pigs (equation 4). An approach is successful (the opponent is displaced) if the relative *Benefit belief* of pig *i* is greater than the value randomly drawn between zero and one. The opponent will be displaced and randomly move to another place in the pen, while the approaching pig starts feeding. An approach is unsuccessful if the value for the *Success probability* is smaller than the value randomly drawn between zero and one. In this case the opponent pig continues feeding, while the approaching pig performs a behaviour related to its second highest motivation or waits.

$$(4) \text{ Success probability} = \frac{\text{Benefit belief}_i}{\text{Benefit belief}_i + \text{Benefit belief}_j} > \text{RND} (0,1)$$

## Feeding

When a pig that is motivated to feed enters an unoccupied feeder, it first determines its rate of feeding. *Feeding rate* (g/min) is based on a physical maximum feeding rate ( $Feeding\ rate_{max}$ ), preferred feeding rate ( $Feeding\ rate_{pref}$ ), *Palatability* of the diet with a fixed value of 0.7, *Feeding drive* and *Group size effect* (equation 5, adapted from Boumans et al. (2015)). Comparable to model of Boumans et al. (2015), it is assumed that a pig has a  $Feeding\ rate_{pref}$ , based on a physical maximum feeding rate ( $Feeding\ rate_{max}$ ) and its *Body weight* (equation 5a,b). *Feeding drive* replaces *Satiation* in the previously used equation since this variable better represents a “hungry pig effect” when a pig is unable to feed for a longer time. Furthermore, a *Group size effect* is included, based on increased *Social pressure* (with a fixed value of 0.5) per additional pig (equation 5c). Social pressure is proposed to cause an increase of feeding rate in group housed pigs (Nielsen, 1999). Pigs might increase their feeding rate to maximize their feed intake in case they are interrupted at the feeder. It might also reduce the chance of an interaction, since they might use the feeder for a shorter time period. We assumed that *Social pressure* is higher in a larger group size and therefore included a fixed value per additional pig (equation 5c) to fit the feeding rate within the empirically observed range in various group sizes.

$$(5) \text{ Feeding rate} = \text{Maximum} \left( \frac{Feeding\ rate_{pref} \times Palatability\ diet}{exp(-0.15 \times Feeding\ drive)} + \text{Group size effect} \right), Feeding\ rate_{max}$$

Wherein:

$$(5a) \text{ Feeding rate}_{pref} = Feeding\ rate_{max} \times Body\ weight^{-0.25}$$

$$(5b) \text{ Feeding rate}_{max} = \frac{(2.85 \times Body\ weight)}{3.6}$$

$$(5c) \text{ Group size effect} = (group\ size - 1) * Social\ pressure$$

If pigs are displaced from the feeder during a time step, this means that more pigs have fed in the same minute. In this case, the feeding rate and feeding time (one minute) of a pig is divided by the number of pigs that fed that minute to calculate the amount of feed intake and feeding time for a pig that time step.

### 5.4.2.3 Growth

At the end of each minute, pigs calculate nutrient and energy use and absorption. Energy remaining after costs for maintenance and activity will be used for body weight growth. See for a detailed explanation Boumans et al. (2017b).

## 5.5 Model analysis

### 5.5.1 Scenario testing

The interaction between social factors (competition and social facilitation) and behavioural strategies (avoid and approach) on feeding and social interaction patterns was tested in four scenarios (Table 2). In scenario 1, pigs avoid competition and postpone feeding till the feeder is free, whereas in scenario 2, pigs approach and displace feeding pigs. Scenario 1 and 2 were created to better understand the specific effect of avoidance and of displacement on feeding patterns and to test whether behavioural strategies chosen in a group explain the change in direction from a turning point onwards. Scenario 3 tests a likely combination of avoidance and approach to competition, where pigs decide on *Benefit belief* to approach or avoid feeding pigs and win or lose based on their *Success probability*. In scenario 4 the effect of social facilitation was added. All scenarios were run for a group size of 1, 2, 5, 10, 15, 20, 25 and 30 pigs (females), whereby group sizes represent varying levels of competitive environments. Each combination of scenario and group size was repeated 15 times. We chose simulation day 30 for analysis, at which the average body weight of pigs was 50 kg. This day was chosen to represent the range of body weight found in empirical studies.

**Table 2.** Scenarios to test the effect of social factors and behavioural strategies on feeding patterns in pigs.

Scenario	Social factor	Competition			Social facilitation
	Behavioural strategy	Increase feeding rate	Avoid	Approach	
1.	Avoid	+	+	-	-
2.	Approach & displace	+	-	+	-
3.	Avoid & approach	+	+	+	-
4.	Avoid, approach & social facilitation	+	+	+	+

### 5.5.2 Sensitivity analysis

We analysed the sensitivity of feeding and interaction to variable and parameter settings (Table 3). Parameter values were changed to 20% above and below the standard value, and variable values were modified. To test the effect of various pig and diet conditions on feeding and social interaction patterns, we included these factors in the analysis. Furthermore, we tested sensitivity of model results to calibrated behavioural parameters. The sensitivity analysis was performed in scenario 4, which also included social facilitation parameters and was the most realistic scenario.

Simulations in the sensitivity analysis were repeated 10 times. This number of runs was sufficient to provide feeding and social interaction patterns with limited variance between simulations.

**Table 3.** Input and output variables in the sensitivity analysis (in scenario 4).

Input variables			Output variables
	Standard value	Changed value	
Pig characteristics			Feed intake (g/day/pig)
Sex	Female	Male, castrated male	Feeding time (min/day/pig)
			Feeding rate (g/min/pig)
			Meal frequency (No./day/pig)
Feeding rate <sub>max</sub>	Equation 5b	Value x 0.8, value x 1.2 <sup>1</sup>	Meal size (g/meal/day/pig)
			Meal duration (min/meal/day/pig)
Cortisol amplitude	0.99	0.79, 1.19	Feeder occupation (%/hour/group)
			Avoidance (No./day/pig)
Diet characteristics			Interaction (No./day/pig)
Digestible energy diet (kJ/g)	14.2	11.36, 17.04	Displaced (No./day/pig)
Digestion duration (min)	180	144, 216	
Behavioural characteristics			
Positive feedback	0.05	0.04, 0.06	
Social pressure	0.5	0.4, 0.6	
Compete threshold	0.2	0.16, 0.24	
Reduced effect feeding motivation (in equation 2)	0.05	0.04, 0.06	
Social facilitation	0.1	0.08, 0.12	

<sup>1</sup> These values represent 20% variation, an additional sensitivity analysis for this variable was performed with 50% variation.

The group size at which feeding patterns reach a turning point in empirical studies may be explained by various pig (e.g. breed) and housing conditions (e.g. diet type) that affect competition levels. To test this effect in the model, an additional sensitivity analysis was performed with larger variation in *Feeding rate*<sub>max</sub> (for the standard value and this value x 0.5 and x 1.5) for every group size between 1 and 30 pigs (*Feeding rate*<sub>max</sub> x 0.5 was run till group size 20 because in larger group sizes pig were not able to reach sufficient feed intake). Maximum feeding rate was chosen as an example because the sensitivity analysis showed that of all tested pig and diet parameters, it had the largest impact on model results. To calculate the group size at turning points in the number of conflicts (which is the sum of avoidance and interaction) in these simulations, the statistical program R (version 3.2.0) was used (R Core Team, 2015). We calculated the sum of squares error per degree of freedom for one linear equation and for two linear equations, in which all possible breaking points were calculated as the intersections between the lines. We selected the group size

with best linear fit (regression line) for two linear lines with the smallest value for sum of squares error per degree of freedom as the breaking (turning) point.

## **5.6 Results**

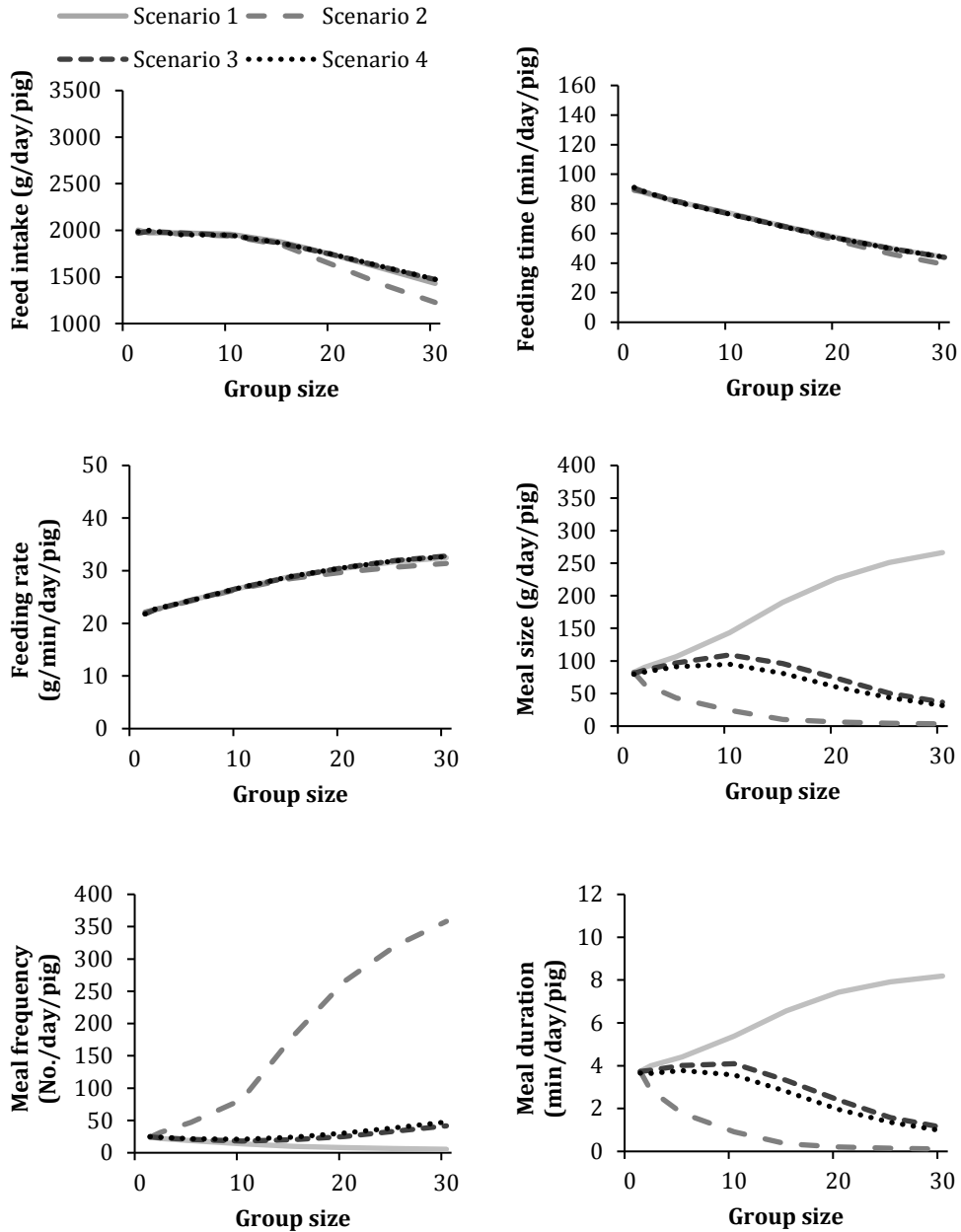
### **5.6.1 The effect of social factors and behavioural strategies on meal-based patterns**

Figure 5 shows the effect of social factors and behavioural strategies on feeding patterns in four scenarios. Patterns of feed intake, feeding time and feeding rate vary slightly between scenarios, whereas patterns of meal size, meal frequency and meal duration vary considerably. Avoidance behaviour in pigs (scenario 1) increased meal size and duration, whereas meal frequency decreased. Approaching behaviour in pigs (scenario 2) resulted in meal patterns completely opposite to those in scenario 1. Feeding patterns in scenario 3 and 4, in which avoidance and approaching are combined, are in between patterns observed in scenario 1 and 2, with a clear turning point in pattern development around group size 10. In smaller groups, meal frequency was lower and meal duration and meal size were higher, whereas in larger groups these patterns showed an opposite development. The addition of social facilitation in scenario 4 affected meal patterns only slightly.

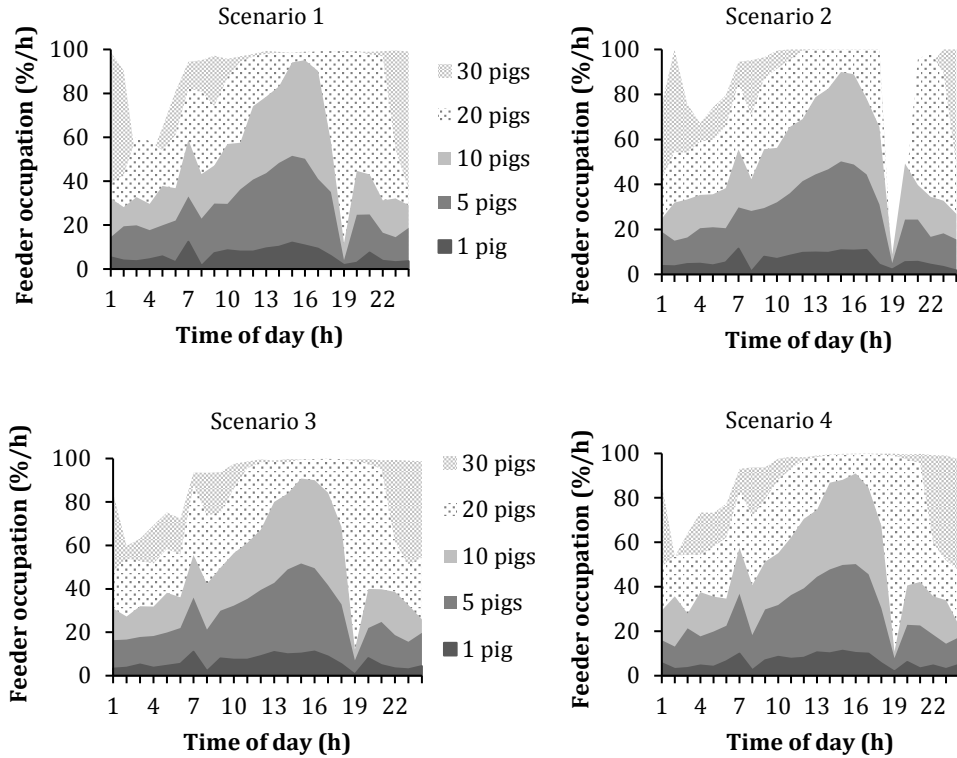
### **5.6.2 The effect of social factors and behavioural strategies on hourly feeder occupation**

For group sizes 1, 5 and 10, hourly feeder occupation was similar in all scenarios (Figure 6). For group size 30, however, feeder occupation was slightly lower in the early morning in scenario 1 and 4. In scenario 2, feeder occupation was 0 at 19:00 h for group size 20 and 30. This is due to a strong increase in melatonin at the beginning of the dark period, which decreased feeding motivation in all pigs simultaneously. This effect of melatonin was visible in scenario 2, because feeding motivation on average was low in this scenario as pigs attempted to feed immediately when hungry. It is likely, however, that in reality this effect will be overruled by higher levels of feeding motivation due to more delay in feeding behaviour, as observed in scenario 1, 3 and 4.





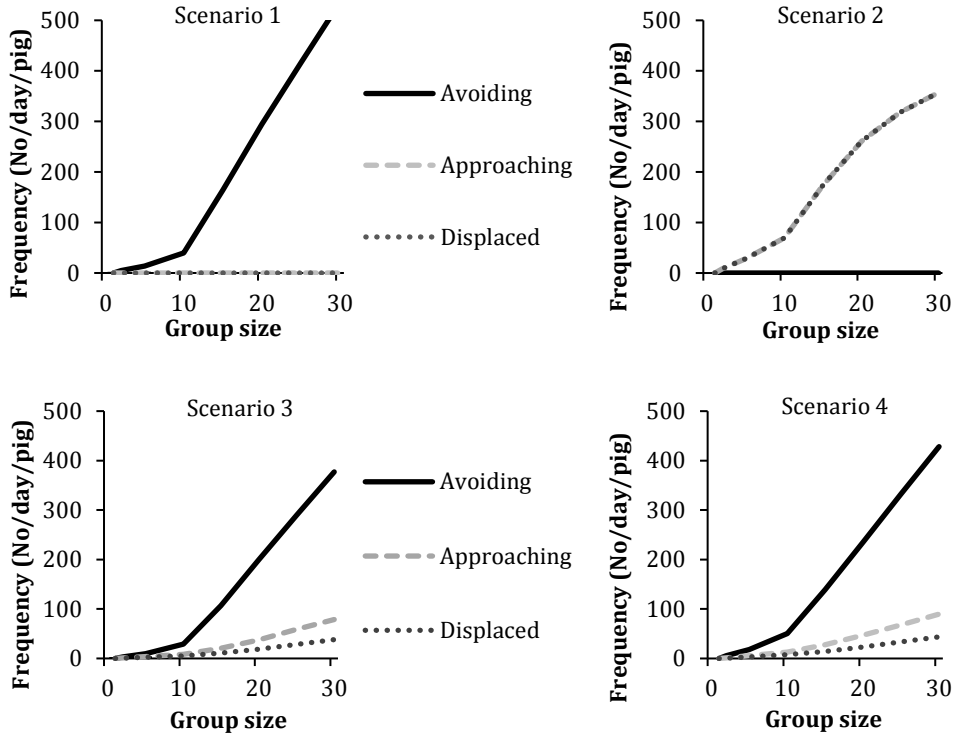
**Figure 5.** Average feeding patterns of pigs in various group sizes in four scenarios: 1) avoid, 2) approach and displace, 3) avoid & approach, and 4) avoid & approach & social facilitation. Each simulation result is an average of 15 simulation runs per combination of scenario and group size.



**Figure 6.** Average hourly feeder occupation in various group sizes in four scenarios: 1) avoid, 2) approach and displace, 3) avoid & approach, and 4) avoid & approach & social facilitation. Each simulation result is an average of 15 simulation runs per combination of scenario and group size.

### 5.6.3 The effect of social mechanisms on social interaction patterns

Social interaction patterns increased with increasing group size in all scenarios, especially in groups larger than 10 pigs (Figure 7). In scenario 1, where pigs avoided each other, avoidance increased linearly in group sizes from 10 pigs onwards. In scenario 2, where pigs approached and displaced each other, displacement increased quadratically from 10 pigs onwards. The patterns in scenario 3 and 4 are relatively similar, but all social interaction patterns are slightly higher in scenario 4.

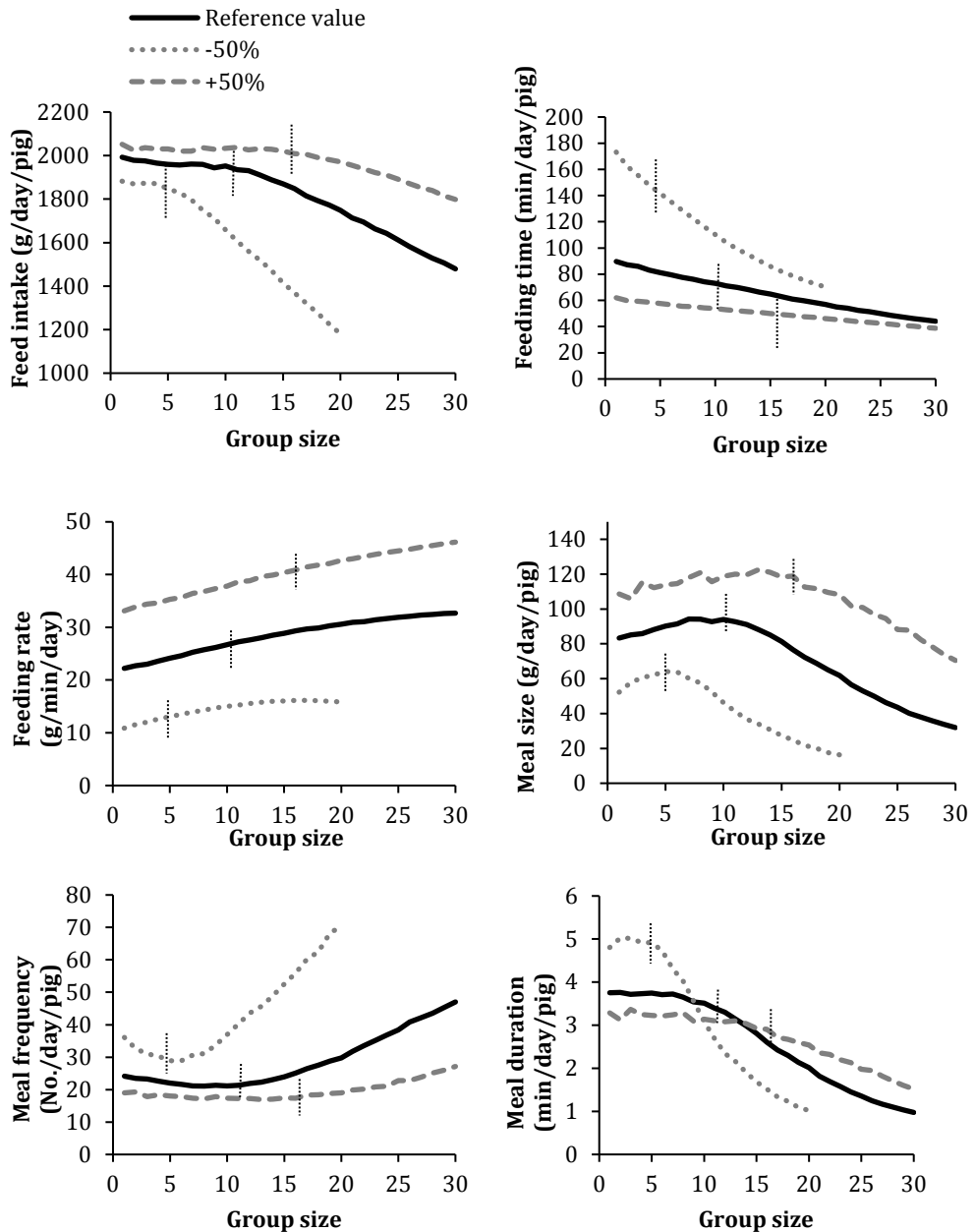


**Figure 7.** Average social interaction patterns of pigs in various group sizes in four scenarios: 1) avoid, 2) approach and displace, 3) avoid & approach, and 4) avoid & approach & social facilitation. Each simulation result is an average of 15 simulation runs per combination of scenario and group size.

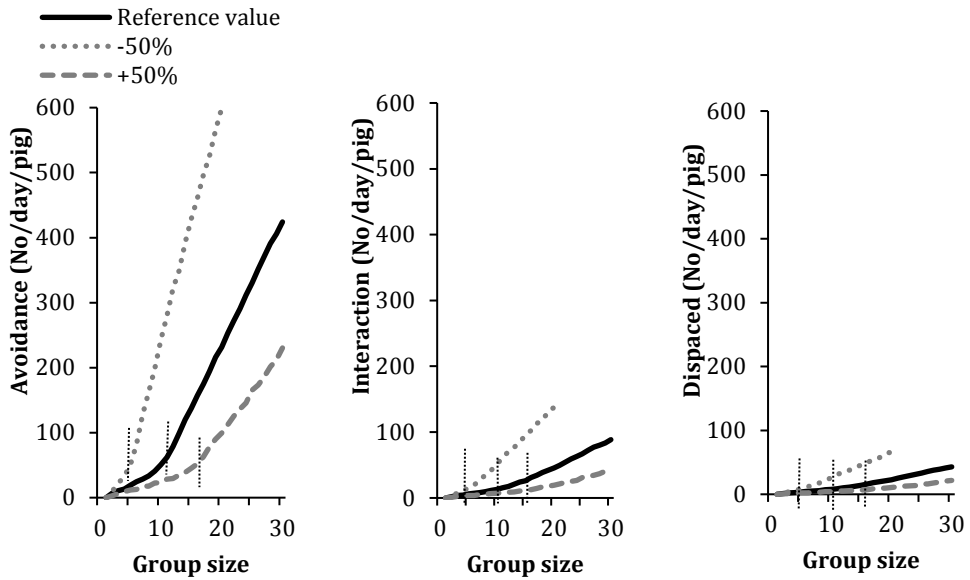
#### 5.6.4 Sensitivity analysis

We analysed sensitivity of the model to variable settings in scenario 4, which is the most realistic scenario. The variables *Digestible energy diet* and *Feeding rate<sub>max</sub>* had the largest impact on feeding and social interaction patterns. Variation in *Digestible energy diet* mainly affected daily feed intake and feeding time in the smallest groups, whereas it mainly affected the meal-based patterns and feeding rate and social interaction patterns in the larger groups (see Appendix, Figure 12). Comparable to *Digestible energy diet*, variation in *Feeding rate<sub>max</sub>* mainly affected daily feeding time in the smallest groups and meal frequency in the largest groups, however, feeding rate and meal size was affected similarly in all group sizes and feed intake was affected more in larger group sizes (see Figure 8 for results with 50% variation in this parameter). The effect on social interaction patterns was comparable between maximum feeding rate and energy level of the diet. Changing other pig and diet variables (*Sex*, *Cortisol amplitude* and *Digestion duration*) and behavioural parameter values (*Positive feedback*, *Social pressure*, *Compete threshold*, *Reduced effect feeding*

*motivation* (in equation 2) and *Social facilitation*) with 20% had an impact of less than 20% on the feeding and social interaction patterns (data not shown).



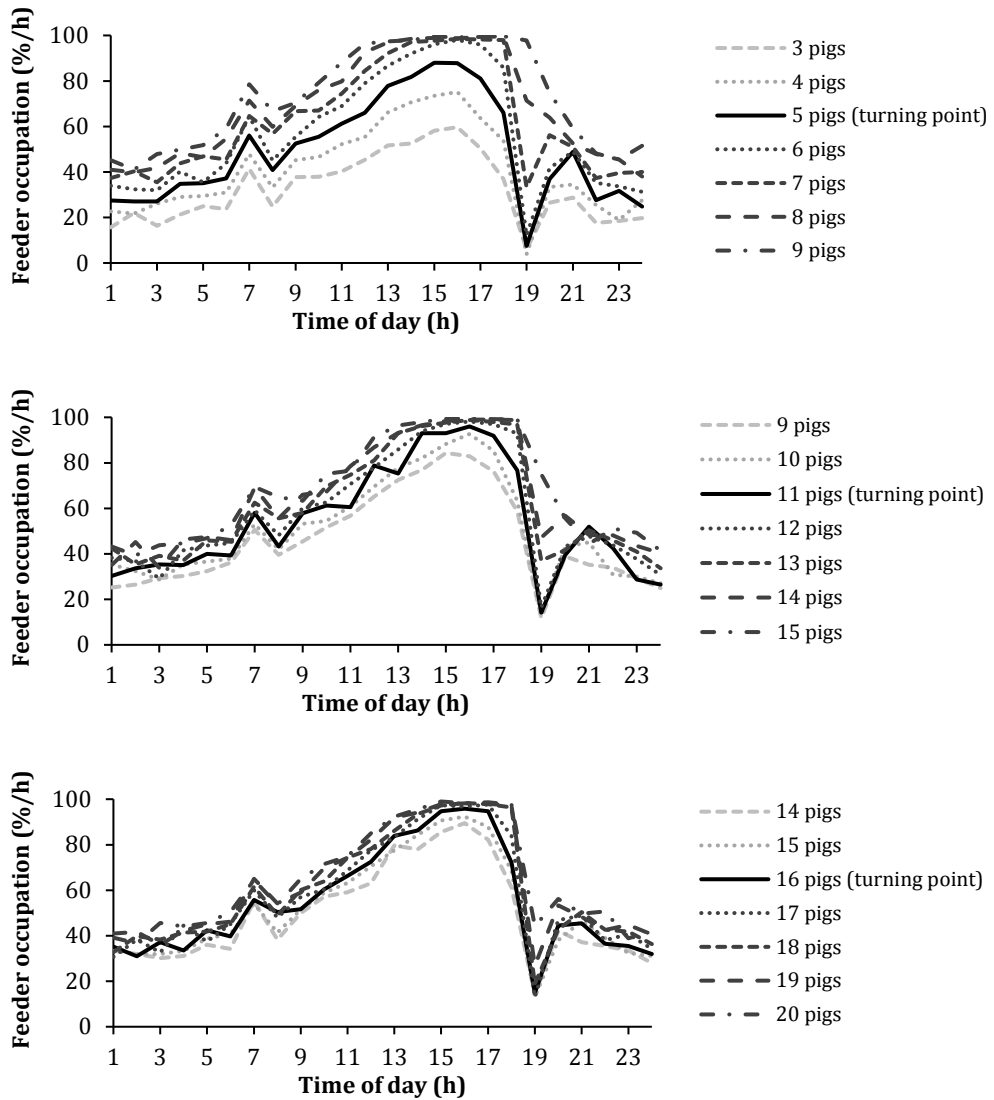
**Figure 8.** Sensitivity analysis of daily feeding patterns to  $Feeding\ rate_{max}$  change of 50% in all group sizes between 1 and 30 pigs. Averages are shown for 10 simulation runs per group size in scenario 4. Vertical dotted lines indicate the group size at which the number of conflicts shows a turning point.



**Figure 9.** Sensitivity analysis of daily social interaction patterns to  $Feeding\ rate_{max}$  change of 50% in all group sizes between 1 and 30 pigs. Averages are shown for 10 simulation runs per group size in scenario 4. Vertical dotted lines indicate the group size at which the number of conflicts shows a turning point.

### 5.6.5 The effect of maximum feeding rate on a turning point

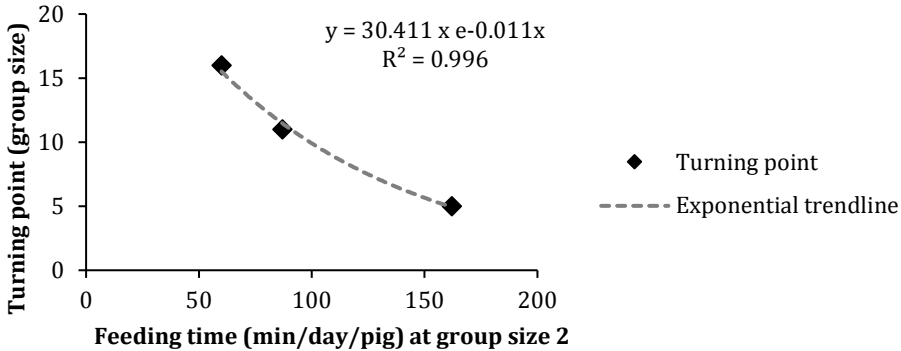
A sensitivity analysis on  $Feeding\ rate_{max}$  was performed with variation of 50% for each group size between 1 and 30 pigs. Results show that  $Feeding\ rate_{max}$  affect group size at which several feeding and social interaction patterns change direction (Figure 8, 9). The turning points in the average number of conflicts were at group size 5, 11 and 16 for the smallest to largest  $Feeding\ rate_{max}$ , respectively.



**Figure 10.** Hourly percentage of feeder occupation time around turning points at various group sizes. Data points are from the sensitivity analysis of  $Feeding\ rate_{max}$  with averages of 10 simulation runs per group size in scenario 4.

Variation in  $Feeding\ rate_{max}$  affected the hourly feeder occupation time in the various group sizes. For all sizes, turning points coincided with similar percentages of hourly feeder occupation time. This percentage was about 35% during night, 60% during the first feeding peak and 80-100% the second peak (Figure 10).

Plotting daily feeding time of pigs (in a group size of 2) and group size at turning points shows an exponential trend (turning point=  $30.411 \times \text{Exp}(-0.011 \times \text{Feeding time of pig at low group density})$ ) (Figure 11). Group size 2 was chosen as smallest group size to represent minimal competition without being affected by other factors such as social isolation stress when pigs are housed individually (Pedersen et al., 2002).



**Figure 11.** The relation between daily feeding time (measured at group size 2) and group size related to turning points in feeding and social interaction patterns in group-housed pigs. Data points are from the sensitivity analysis of *Feeding rate<sub>max</sub>* with averages of 10 simulation runs per group size in scenario 4.

## 5.7 Discussion

We studied the interactions among physiological factors, social factors and behavioural strategies in an ABM to deepen our understanding of mechanisms underlying feeding and social interaction patterns in animals, with pigs as a case study. Emergent feeding and social interaction patterns of pigs in the model were compared with empirical patterns. Feeding patterns in pigs varied considerably between empirical studies (e.g. De Haer & de Vries, 1993b; De Haer & Merks, 1992; Hyun & Ellis, 2001, 2002; Nielsen et al., 1995; Walker, 1991). Patterns of feed intake, feeding time and feeding rate varied in absolute level but showed similar trends with increasing group size. Furthermore, the absolute level variation in patterns of daily feeding time between studies decreased with group size. Various factors are known to contribute to variation in feeding patterns in pigs, such as pig and diet characteristics (e.g. Brouns et al., 1994; De Haer & de Vries, 1993a; Quiniou et al., 2000). Energy level of the diet and maximum feeding rate represented such factors in the model. The sensitivity analysis showed that these factors affected physiological processes in the model and explained the variation in patterns of daily feed intake, daily feeding time and feeding rate between studies, especially in smaller groups. These variables mainly changed the slope of the feeding patterns, without affecting the patterns much.

In contrast to the above mentioned feeding patterns, meal-based patterns (meal frequency, meal duration and meal size) varied not only in absolute level, but also in trends between empirical studies, especially in larger groups. Although initially there seemed no logical explanation for this variation, model results show that behavioural strategies of pigs can explain these results. Pigs in larger groups experienced more competition and conflicts around the feeder, in which they had to decide to avoid or approach these conflicts. An increase in meal size and duration, and decrease in meal frequency was explained in the model by pigs that chose to avoid conflicts, as shown in scenario 1. Simulations in which pigs chose to approach and displace other pigs, however, resulted in opposite meal-based patterns, as shown in scenario 2. This suggests that decreasing meal size and duration and increasing meal frequency patterns indicate a competitive environment with high displacement levels, whereas opposite patterns indicate a low competitive environment with low displacement levels.

Model results thus indicate that pig and diet characteristics mainly explain patterns of feed intake, feeding time and feeding rate, while behavioural strategies of individuals explain variation in patterns of meal frequency, meal duration and meal size. The effect of behavioural strategies was especially evident in larger groups from a certain group size (turning point) onwards, where meal-based and social interaction patterns changed direction. These turning points were also observed in empirical studies, although the group size related to this point seems to vary between studies. Hyun and Ellis (2001, 2002), for example, showed an early turning point around groups of 4 to 8 pigs, whereas Nielsen et al. (1995) found a turning point around 10 to 15 pigs. Our model results explain this turning point by variation in daily feeding time between pigs, which affects feeder occupation time and therefore competition levels in groups. The sensitivity analysis showed that increased daily feeding time in pigs moved the turning point to a lower group size, whereas decreased daily feeding time elevated it. This is in agreement with empirical studies, where pigs with a lower daily feeding time (i.e. 68 minutes per pig per day) showed a turning point in meal-based patterns at a larger group size (i.e. around 10 to 15 pigs) in Nielsen et al. (1995), while pigs with a higher daily feeding time (i.e. 130 minutes per pig per day) showed a turning point at a smaller group size (i.e. around 4 to 8 pigs) in Hyun and Ellis (2001). Feeder occupation, therefore, was also higher in Hyun and Ellis (2001) than in Nielsen et al. (1995). This might explain why daily feed intake decreased and the number of displacements increased in the largest groups in the study of Hyun and Ellis (2001), even though group sizes in that study (2, 4, 8 and 12) were on average small and would not suggest high competition levels.

Following the reasoning above, this suggests that reducing feeding time is a potential first adaptation to reduce competition for a food resource in group housing. A pig can reduce its feeding time by reducing its daily feed intake or increasing its feeding rate.



It is assumed that pigs desire to obtain a certain level of daily feed intake, therefore, an increase of feeding rate is a likely adaptation to competition (Nielsen, 1999). The ability to increase feeding rate, however, can be different among pigs because of physical limitations, such as feed intake capacity of the mouth (Illius & Gordon, 1987). In addition, this ability increases to a certain extent with increasing body weight. Pigs that are physically limited, therefore, have a higher risk of not reaching the desired daily feed intake. This is shown in the studies of Hyun and Ellis (2001, 2002), where a smaller response in feeding rate was the main difference between growing and finishing pigs, and the smaller growing pigs were not able to maintain daily feed intake levels, whereas the larger finishing pigs were (Hyun & Ellis, 2002). Furthermore, the feeding patterns in the sensitivity analysis with a 50% decrease of maximum feeding rate are in agreement with the patterns in the study of Hyun and Ellis (2001), which confirms that a factor such as limited feeding rate can explain the feeding patterns in that study.

The sensitivity analysis with variation in maximum feeding rate for each group size showed that with default model parameters, the turning point emerged at group size 11 in scenario 4. With a 50% lower feeding rate, however, the turning point emerged at group size 5, whereas with a 50% higher feeding rate it emerged at group size 16. These turning points showed an exponential relation with feeding time of pigs, suggesting that feeding time of a pig housed in a small group can predict at which group size competition levels for a food resource would increase, and, hence, a turning point in feeding and interaction patterns would emerge. Based on the observed average daily feeding time of 130 minutes in Hyun and Ellis (2001) and 118 minutes per pig in Hyun and Ellis (2002) in group size 2, the turning points for these studies were calculated at 7.3 and 8.3 pigs respectively. These turning points fit in the observed feeding patterns of these studies. Furthermore, the turning point of 7.3 is in agreement with the amount of displacements in the study of Hyun and Ellis (2001), which were significantly higher for group size 8 and 12. The turning point (based on an average feeding time of 68 minutes in the smallest group size of 5 pigs) for the study of Nielsen et al. (1995), was calculated at a group size of 14.4 pigs. This value is comparable with the empirical data, where patterns of meal frequency, meal duration and meal size were significantly different between group size 5 to 15 and group size 20. That increased competition above group size 15 did not affect displacement behaviour in that study, can be explained by a high level of avoidance as behavioural strategy. This was also confirmed by the feeding patterns in that study, which were similar to the feeding patterns in scenario 1, where pigs did not compete. The high level of avoidance behaviour can be related to pig characteristics, such as coping style and aggression level, or group dynamics, such as a clear and stable social hierarchy.

Besides daily feeding time, also the hourly feeder occupation distribution seems to be related to turning points. Hourly feeder occupation in group size 8 reached 50%

during the night and 80% during the day in the study of Hyun and Ellis (2001), and 50% during the night and 90% during the day in group size 20 in the study of Nielsen et al. (1995). In both studies, a proportionally larger increase in nightly than in daily feeder occupation was observed in group sizes below and above this turning point. The simulation results were in line with these empirical results, and suggest a relation between a turning point and an hourly feeder occupation time above 35% during the night, and above 80% during the highest day peak.

We expected that social facilitation would stimulate behavioural synchrony in feeding behaviour and explain the more clumped distribution of feed intake during day time in group housed pigs compared to the more equal distribution in individually housed pigs. This more clumped distribution, however, also occurred in scenarios without the mechanism of social facilitation. Furthermore, the addition of social facilitation in scenario 4 showed no further clumping effect. This suggests that a clumped distribution of feed intake is more likely caused by physiological factors, such as daily energy balance and hormonal circadian rhythms, than by social factors, such as social facilitation and behavioural synchrony. Social facilitation only slightly decreased meal duration and meal size, and increased meal frequency and interactions in scenario 4. This suggests that social facilitation slightly increases competition, but plays a minor role in feeding patterns in group-housed pigs with one feeding place. This is comparable to the findings in laying hens of Collins et al. (2011), who concluded that social facilitation affects behavioural synchronicity and clustering around a feeder, but that this behaviour is mainly resource driven rather than socially driven. For group-housed pigs, the minor effect of social facilitation might also be due to experience, in which pigs have learned that only one pig can feed at the time and there is no use in responding to a social facilitation stimulus.

In this paper we presented a mechanistic ABM, in which feeding and social interaction patterns emerge from a complex interaction between physiological, behavioural and environmental factors. The model was built stepwise, whereby first internal processes, such as metabolic and endocrine processes affecting growth and feeding motivation, were modelled and validated (Boumans et al., 2015; Boumans et al., 2017b). In the current study, social factors and group dynamics were added to the model, allowing to gain more insight in the complexity of internal and external factors underlying pig behaviour. The integration of factors from various disciplines (e.g. nutrition, energetics, endocrinology and ethology) and the level of detail allows to compare the model with a wide range of empirical patterns for validation. The large number of patterns that are comparable between the model and empirical data and the validation of the model in several phases, give confidence that the model contains the appropriate mechanisms.

Our study shows how physiological factors can affect interactions and behavioural patterns (e.g. affect competition levels at certain times and affect behaviour such as feeding rate) and increases our understanding of behaviour. The relation between a physiological state of an animal and its behaviour, as included in our model, is studied relatively little, although physiological influence on animal behaviour is becoming increasingly evident nowadays (Jachowski & Singh, 2015). This model can be used as a tool in further research to study the effect of social factors and group dynamics on individual variation in feeding and social interaction patterns. Our model allows, for example, to study contradictory and ill-understood empirical patterns in meal frequency and meal duration of dominant and subordinate animals, such as observed in pigs (e.g. Hoy et al., 2012). In our step-by-step approach, we can gradually test potential explanatory factors, such as group composition, individual coping styles and hierarchical stabilities, and disentangle their effect on behaviour.

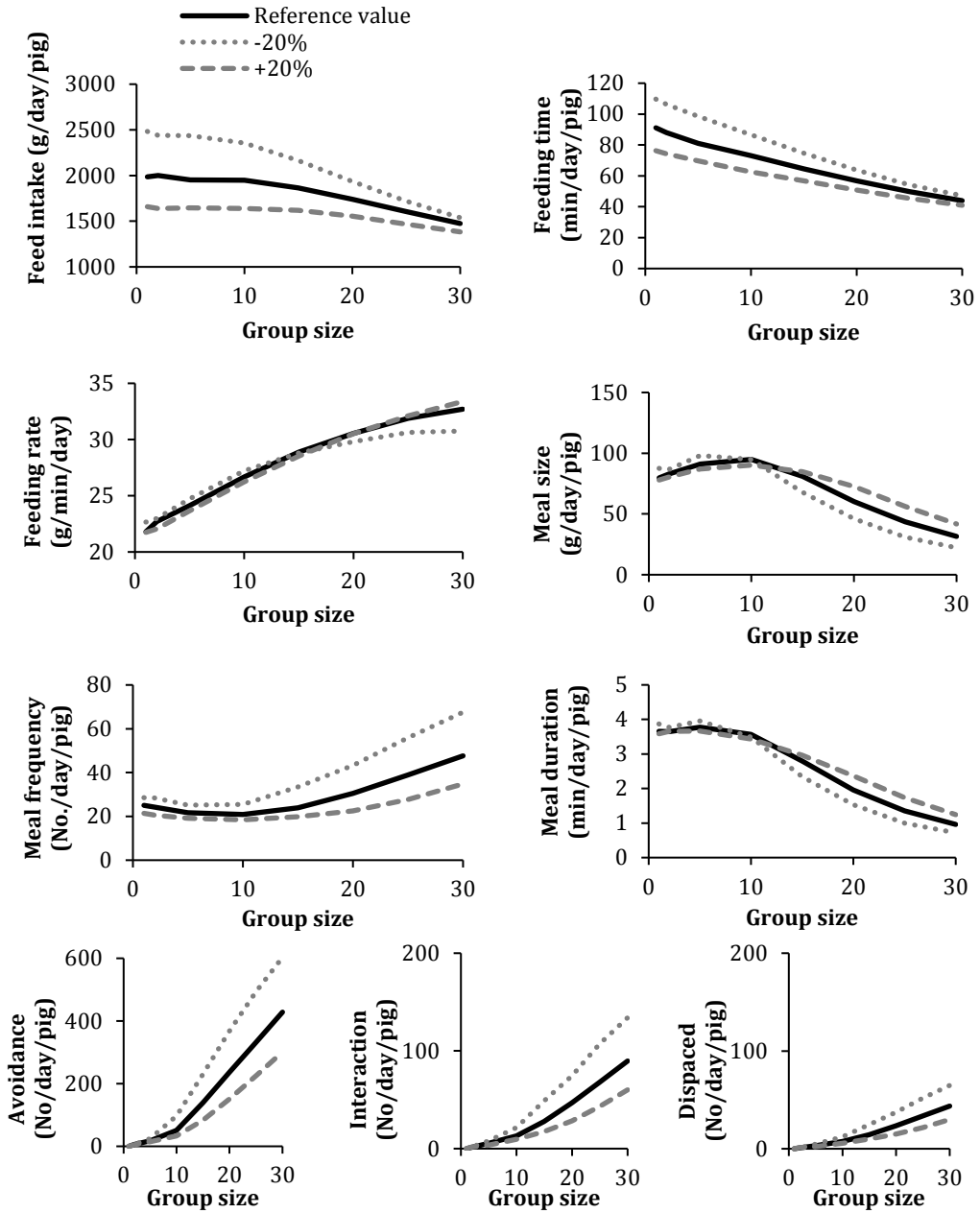
The use of agent-based modelling in understanding animal behaviour in combination with a relatively detailed level of physiological factors is novel in research. We believe that this approach can be valuable in further studies in animal behaviour. Although the model was developed for pigs, the included factors are likely important in the behaviour of many animal species. Model values can be adjusted and mechanisms can be changed to fit characteristics, for instance, for other farm animals in a similar environment or wild animal species in environments where food resources are scarce or easily defensible.

To conclude, our study increased understanding of feeding and social interaction patterns in animals and underlying mechanisms. The ABM results suggest that the social factor 'competition' largely determines at what group size a turning point in feeding and social interaction patterns emerges. Below a turning point, competition between pigs is affected by pig and diet characteristics. These pig and diet characteristics affect patterns of daily feeding time, daily feed intake and feeding rate, and explain the majority of the variation in these patterns between empirical studies. Daily feeding time of pigs appeared a good indicator to predict the group size at which a turning point in feeding and social interaction patterns emerges. A feeder occupation above 35%/h during the night and 80%/h during the day can also indicate a turning point in patterns. Beyond that turning point, conflicts between pigs occur more commonly and behavioural strategies to adapt to these conflicts mainly explain variation between empirical studies in meal-based and social interaction patterns. Social facilitation can increase competition, but appeared unimportant in the causation of feeding and social interaction patterns of pigs in the model. The modelling approach used in this study can be valuable for gaining more understanding of mechanisms underlying patterns of animal behaviour.

### **Acknowledgements**

We would like to thank Aart van der Linden and Cindy Klotwijk for advice in model analysis and Lia Hemerik for advice and writing code in R to calculate breaking points in our model data. This research was funded by the IP/OP program 'Complex Adaptive Systems' of Wageningen UR.

## Appendix



**Figure 12.** Sensitivity analysis of daily feeding and social interaction patterns to diet energy parameter change of 20% in various group sizes. Averages are shown for 10 simulation runs per group size in scenario 4.



# Chapter 6

## **Unravelling variation in feeding, social interaction and growth patterns among pigs using an agent-based model**

Iris J.M.M. Boumans<sup>a</sup>, Imke J.M. de Boer<sup>a</sup>, Gert Jan Hofstede<sup>b</sup>, and Eddie A.M. Bokkers<sup>a</sup>

<sup>a</sup> Animal Production Systems group, Wageningen University, Wageningen, the Netherlands

<sup>b</sup> Information Technology group, Wageningen University, Wageningen, the Netherlands

This chapter has been submitted

## **Abstract**

Domesticated pigs, *Sus scrofa*, vary considerably in feeding, social interaction and growth patterns. This variation originates partly from genetic variation that affects physiological factors and partly from behavioural strategies (avoid or approach) in competitive food resource situations. Currently, it is unknown how variation in physiological factors and in behavioural strategies among animals contributes to variation in feeding, social interaction and growth patterns in animals. The aim of this study was to unravel causation of variation in these patterns among pigs. We used an agent-based model to explore the effects of physiological factors and behavioural strategies in pigs on variation in feeding, social interaction and growth patterns. Model results show that variation in feeding, social interaction and growth patterns are caused partly by chance, such as time effects and coincidence of conflicts. Furthermore, results show that seemingly contradictory empirical findings in literature can be explained by variation in pig characteristics (i.e. growth potential, positive feedback, dominance, and coping style). Growth potential mainly affected feeding and growth patterns, whereas positive feedback, dominance and coping style affected feeding patterns, social interaction patterns, as well as growth patterns. Variation in behavioural strategies among pigs can reduce aggression at group level, but also make some pigs more susceptible to social constraints inhibiting them from feeding when they want to, especially low-ranking pigs and pigs with a passive coping style. Variation in feeding patterns, such as feeding rate or meal frequency, can indicate social constraints. Feeding patterns, however, can say something different about social constraints at group versus individual level. A combination of feeding patterns, such as a decreased feed intake, an increased feeding rate, and an increased meal frequency might, therefore, be needed to measure social constraints at individual level.

**Keywords:** growing pigs; feeding behaviour; group dynamics; welfare; productivity; simulation.



## 6.1 Introduction

Behavioural feeding patterns, such as feed intake, meal frequency, meal duration and meal size, vary considerably across domesticated pigs, *Sus scrofa* (e.g. De Haer & Merks, 1992; Hoy et al., 2012; Nielsen et al., 1996a). Although each animal is assumed to reach a certain level of daily food intake, the strategy to reach this differs among animals (Fernández et al., 2011; Nielsen, 1999). Scientific literatures suggests four main feeding patterns in pigs, based on meal frequency, meal duration, and feeding rate (Fernández et al., 2011). Pigs with few long meals are described as meal eaters, pigs with many short meals as nibblers, pigs with a low feeding rate as slow eaters and pigs with a high feeding rate as fast eaters.

Variation in feeding patterns among pigs partly originates from genetic variation and, therefore, is associated with breeds (Fernández et al., 2011). Genetic variation can affect pig characteristics, such as growth capacity or stomach size, which can affect physiological processes underlying feeding behaviour, and consequently body weight (Boumans et al., 2015; Boumans et al., 2017b). During the growing period, pigs gradually shift from nibblers and slow eaters to meal and fast eaters (Bigelow & Houpt, 1988), which can be explained by change in body weight (Boumans et al., 2015).

Pigs of the same breed with a similar body weight, however, still show variation in feeding patterns. In crossbred Landrace x Large White pigs with similar weight, for example, both meal eaters and nibblers were identified (Nielsen et al., 1996a). Boumans et al. (2017a) argued that this kind of variation might result from competition among pigs for feed resources and related behavioural strategies (avoid or approach behaviour). Pigs that avoid conflicts or lose fights, for example, can have limited access to feed in a competitive environment and, therefore, might shift from a meal and slow eater type to a nibbler and fast eater type. In a previous study, we showed that competition can affect feeding rate, whereas behavioural strategies in a feed competitive environment can affect meal patterns, such as meal frequency and duration (Boumans et al., 2017a).

Currently, it is unknown how variation in physiological factors and in behavioural strategies among pigs contributes to variation in feeding, social interaction and growth patterns among animals. In empirical studies, researchers have tried to explain variation in these patterns based on dominance order. Dominant pigs approached and displaced other pigs more often at the feeder, whereas subordinate pigs are displaced more often at the feeder and showed more but shorter visits to the feeder than dominant pigs (Hoy et al., 2012). Feeding patterns were reversed in a study of Leiber-Schotte (2009), where subordinate boars had fewer and longer meals than dominant boars. Both dominant and subordinate pigs showed high and low feeding visits and displacement attempts in a study of Nielsen et al. (1996a). The

relation between dominance rank, feeding patterns and social interaction patterns, thus varies between studies. Furthermore, growth rates over the whole growing period were lower for dominant pigs in the study of Leiber-Schotte (2009), whereas they were similar for dominant and subordinate pigs in the study of Hoy et al. (2012). This suggests that dominance is important in behavioural strategies, but not fully explains variation in feeding, social interaction and growth patterns of individuals.

Another pig characteristic that potentially might affect behavioural strategies is coping style. Coping styles are regarded as consistent behavioural and physiological responses of animals to environmental challenges (Koolhaas et al., 1999). Two typical behavioural coping styles are observed: an aggressive and (pro)active coping style, and a non-aggressive and passive coping style (e.g. Bolhuis et al., 2005b; Camerlink et al., 2016; Koolhaas et al., 1999). Although the effect of coping styles on feeding patterns in pigs has hardly been studied, typical behaviour associated with coping styles might explain variation in feeding, social interaction and growth patterns in pigs.

The aim of this study was to unravel causation of variation in feeding, social interaction and growth patterns among pigs. We hypothesised that interaction between physiological factors and behavioural strategies of individuals can cause variation and can explain the contrasting results in empirical studies. Understanding individual variation is an intensively studied topic in many feral animal species (Réale et al., 2007; Sih et al., 2004; Wolf & Weissing, 2010). It is also relevant for domestic farm animals if we want to better understand the capacity of animals to cope with environmental factors and their susceptibility to stressors (Koolhaas & van Reenen, 2016).

Since it is difficult to unravel effects of internal and external factors on individual variation via empirical studies, we used an agent-based model (ABM) to explore the effects of physiological factors and behavioural strategies in pigs on variation in feeding, social interaction and growth patterns among pigs. We specifically addressed the following research questions:

1. What is the effect of individual variation in physiological factors on feeding, social interaction and growth patterns?
2. What is the effect of individual variation in behavioural strategies on these patterns?
3. Can interaction between physiological factors and behavioural strategies explain empirically observed variation among pigs?

## 6.2 Material & methods

### 6.2.1 Model description

We used an existing ABM on feeding and interaction behaviour of growing pigs that had been developed in previous studies (Boumans et al., 2015; Boumans et al., 2017a; Boumans et al., 2017b). The model simulates the emergence of feeding, social interaction and growth patterns of group-housed pigs based on physiological factors (e.g. processing of feed, energy absorption, energy use for maintenance, activity and growth, circadian rhythms of melatonin and cortisol) and social factors (competition and social facilitation). Due to variation in pig characteristics (e.g. growth potential and coping style) various patterns emerge. The model was developed in Netlogo 5.3 (Wilensky, 1999). The main aspects of the model are described below. For a detailed explanation see Boumans et al. (2017a). Furthermore, the model and a detailed model description are available on the OpenABM website (<http://www.openabm.org>).

### 6.2.2 Design concepts

The model is based on the concept of motivation for behavioural decision-making: internal and external factors affect motivation that causes a behaviour, in which performance of the behaviour has feedback effects (Jensen & Toates, 1997). Internal factors include digestion of feed, metabolism, circadian hormonal rhythms and pig characteristics, which affect feeding motivation via their effect on feeding drive and satiation. External factors include feed, water, temperature, light and group mates. Motivation for a specific behaviour consists of an energy drive and threshold level that are affected by these internal and external factors (Hogan, 1997). Subsequently, motivations for several behaviours are compared, in which the highest motivation causes the behaviour, described as the state-space approach by McFarland and Sibly (1975). Performed behaviours affect the energy use and intake of a pig, and its growth; and provide feedback to motivation. Feeding, growth and social interaction patterns emerge due to interaction between the above-mentioned factors in the model.

### 6.2.3 Agents, environment, state variables and scales

Table 1 shows the main state variables and their standard values. The model environment represents ten conventionally group-housed agents (pigs) in a barren pen, comparable to a commercial growing pigs housing system. Objects in the pen, besides agents, are a feeder and a drinker. Water and feed are accessible *ad libitum*. Light and temperature in the pen are based on values commonly found in empirical studies. The feed represents a commercial diet for growing pigs based on values from NRC (2012) on required dietary amino acids, protein and digestible energy. In the current study, pigs represented female growing pigs and started with a body weight of

**Table 1.** Main input state variables and standard (initial) values in the model.

Parameter	Value
<i>Environment</i>	
Feeders (No)	1
Drinkers (No)	1
Group size (No)	10
Temperature ( °C)	22
Start light period (h)	06:00
Start dark period (h)	18:00
<i>Diet characteristics</i>	
Digestible energy content diet (kJ/g)	14.2
Dietary amino acid content Lysine (g/kg)	11
Dietary amino acid content Methionine (g/kg)	3
Dietary amino acid content Methionine + Cystine (g/kg)	6
Dietary amino acid content Threonine (g/kg)	6
Dietary amino acid content Tryptophan (g/kg)	2
Dietary amino acid content Isoleucine (g/kg)	5
Dietary protein content (g/kg)	132
Apparent amino acid and protein availabilities	0.82
Palatability diet	0.7
<i>Pig characteristics</i>	
Sex	Female
Initial body protein weight (kg)	4
Minimum body lipid to body protein ratio (kg/kg)	1
Mean body protein deposition (g/day for gilts)	137
Cortisol amplitude	0.99
Melatonin night	0.8
Melatonin day	0.4
Positive feedback	0.25
Dominance value	15
Compete threshold	0.3
<i>Social (group) characteristics</i>	
Social facilitation effect	0.1
Social pressure (feeding rate increase in g/min)	0.5

28 kg (based on an initial body protein weight of 4 kg). Growth capacity of pigs in the model is based on their capacity to deposit body protein and their minimum body lipid to protein ratio (De Lange, 1995; NRC, 2012). Pigs have a hormonal circadian rhythm of cortisol and melatonin that affects their energy use and motivation (Boumans et al., 2017b). Positive feedback temporarily increases feeding motivation and stimulates a pig to reinforce feeding behaviour in a next time step. The value of 0.25 for this parameter was increased compared to Boumans et al. (2017a) to allow a better assessment of the individual variation effect. Social facilitation increases

feeding motivation of all other pigs when a pig is feeding and can stimulate competition (Boumans et al., 2017a). Competition between pigs for access to a feeder can cause conflicts, in which pigs can choose to interact with each other. Pigs have a dominance value that represented the social rank of a pig in the dominance hierarchy with group mates. The value of 15 corresponds to the initial value in Hemelrijk (2000). Compete threshold represents a coping style of a pig in a conflict situation and is a value that affects the probability of a hungry pig to approach an opponent pig at the feeder. Social pressure increases the feeding rate of a pig. Time steps in the model represent one minute within a day of 1440 minutes. Simulations were run for 14 days, which corresponds to the experimental period in the study of Nielsen et al. (1996a).

#### **6.2.4 Process overview**

During each time step, pigs are evaluated in three submodels: *Motivation*, *Behaviour* and *Growth*.

The submodel *Motivation* includes the calculation of feeding motivation and other behavioural motivations (exploring, drinking or lying). The other behavioural motivations are included to simulate energy use and are based on a drive and threshold that changed every time step. Feeding motivation is included more in depth and is the result of feeding drive and satiation, based on physiological parameters such as stomach load, (instant and daily) energy absorption and requirement. These physiological parameters are affected by circadian patterns of cortisol and melatonin, which vary during the day and affect the daily energy balance and feeding drive. Additionally, feeding motivation of pigs can increase due to feeding behaviour of a group mate, known as a social facilitation effect (Clayton, 1978).

The submodel *Behaviour* includes the performance of a behaviour based on the highest motivation. These behaviours include feeding, exploring, drinking or lying. Feeding behaviour can be blocked or disturbed by other pigs. In case of conflicts, hungry pigs can decide to avoid or approach (attempt to displace) other pigs, and feeding pigs can be displaced or resist displacement and continue feeding. In a conflict, pigs choose their response based on their *Dominance value*, *Compete threshold* and feeding motivation, in which a social higher rank, an active coping style and more hunger will more likely cause an displacement attempt of a hungry pig. When a feeding motivated pigs occupies a feeder, it determines its feeding rate based on a preferred feeding rate (affected by body weight), palatability of the diet and feeding drive. Social pressure (group size effect) can increase the feeding rate of a pig with 0.5 g/min per additional pig in the group, but feeding rate cannot exceed a maximum (physically constrained) feeding rate based on body weight.

The submodel *Growth* calculates nutrient absorption due to digestion and nutrient use for body maintenance, activity and growth per time step. Body weight of pigs is then

recalculated based on their nutrient use and intake and growth capacity. Growth capacity depended on their *Mean body protein deposition* and the ratio of protein and lipid in the body.

### 6.2.5 Simulation experiments

Pig characteristics were individually varied in four parameters: *Mean body protein deposition*, *Positive feedback*, *Dominance value* and *Compete threshold*. The first two parameters were chosen to represent variation in physiological factors. The parameter *Mean body protein deposition* represents growth potential and was chosen to affect variation among pigs in the given level of feed intake that a pig aims to reach daily. The parameter *Positive feedback* was chosen to represent meal frequency and duration as it was known that it had a large impact on these patterns in the model (see results of Boumans et al., 2015). This parameter might, for example, reflect the capacity of the stomach for feed intake and stimulate longer or shorter meals. The last two parameters, *Dominance value* and *Compete threshold*, were chosen to affect variation in behavioural strategies. *Dominance value* represented dominance rank and *Compete threshold* represented coping style. These parameters were selected because they are assumed to have a large impact on variation in behavioural strategies (conflict avoidance and approach) without being related to each other. A pig with a more aggressive coping style is not necessarily the most dominant pig in the group that wins fights (Bolhuis et al., 2005b; Camerlink et al., 2016), but coping style may affect displacement (attempts) of pigs at the feeder and therefore affect social interaction patterns.

**Table 2.** Scenarios to test the effect of time and individual variation in pig characteristics on feeding, social interaction and growth patterns in groups of 10 pigs.

Scenario	Mean value of parameters				Percentage of the mean value as standard deviation			
	Mean body protein deposition	Positive feedback	Dominance value	Compete threshold	Mean body protein deposition	Positive feedback	Dominance	Compete threshold
1. No variation in parameters	137	0.25	15	0.3	0	0	0	0
2. Growth potential	137	0.25	15	0.3	10	0	0	0
3. Meal type	137	0.25	15	0.3	0	30	0	0
4. Dominance	137	0.25	15	0.3	0	0	30	0
5. Coping style	137	0.25	15	0.3	0	0	0	30
6. Combined variation	137	0.25	15	0.3	10	30	30	30

We simulated six scenarios to test the effect of individual variation in physiological factors and behavioural strategies in the model on feeding, social interaction and growth patterns (Table 2). Scenario dependent, parameter values were equal for all pigs (i.e. the mean value) or varied among individuals. If varied, parameter values were randomly assigned to pigs within a pen based on a normal distribution with the mean value of that parameter as average and a standard deviation that consisted of a percentage of the mean value. In scenario 1, the four parameters were set equal for all pigs to test to which extent variation in feeding, social interaction and growth patterns is a result of time and competition, rather than the effect of individual variation in pig characteristics and strategies. In scenario 2, 3, 4 and 5 the effect of variation in one parameter was tested. Individual variation depended on randomly assigned parameter values to pigs based on a normal distribution with the standard value as mean and a standard deviation that consisted of a percentage of the mean value. A standard deviation of 10% for *Mean body protein deposition* was chosen to fit within the range of empirically observed variation in daily protein deposition rates (e.g. Quiniou et al., 1996). A standard deviation of 30% for *Positive feedback* was chosen to create individual variation in which values can also come close to zero. A standard deviation of 30% for *Dominance value* was chosen to correspond to the distribution in Hemelrijk (2000). A standard deviation of 30% for *Compete threshold* was also chosen to create a range in which values can come close to zero. To prevent a negative value, parameter values of *Positive feedback*, *Dominance value* and *Compete threshold* that were below zero were set to 0.001. In scenario 6, a combination of variation in all 4 parameters was tested. The scenarios were simulated in the standard settings of the model with parameter values as described in Table 1.

Sensitivity of the model was tested to the value level of the four chosen parameters (*Mean body protein deposition*, *Positive feedback*, *Dominance value* and *Compete threshold*) and to the variation among individuals in values for this parameter (Table 3). Scenario 1 was selected to test the effect of parameter values when all values were equal for pigs. The value of each parameter was increased and decreased with 20% from the standard value in a local sensitivity analysis (thus with change of one parameter value per simulation). Sensitivity of the model to variation among individuals in parameter values was tested in scenario 6, in which parameter values were different for all pigs representing the scenario closest to a real existing scenario. The standard deviation in the normal distribution when parameter values were assigned to pigs was increased or decreased with 50% (thus changing the range of variation among individuals). In addition to the four parameters, group size was increased and decreased with 50% (group size 5 and 15) in scenario 6 to test the effect of competition level (i.e. incidence of conflicts). All simulations in this study were run for 14 days and were repeated 50 times.

**Table 3.** Sensitivity analysis to test the effect of parameter values and variation of parameter values among individuals on emerged patterns. Changed parameter setting are indicated in bold values.

Scenario – parameter – change %	Mean value of parameters					Percentage of the mean value as standard deviation			
	Group size	Mean body Protein deposition value	Positive feedback	Dominance value	Compete threshold	Mean body protein deposition	Positive feedback	Dominance value	Compete threshold
Sc.1 – Mean body protein dep. -20%	10	<b>110</b>	0.25	15	0.3	0	0	0	0
Sc.1 – Mean body protein dep. +20%	10	<b>164</b>	0.25	15	0.3	0	0	0	0
Sc.1 – Positive feedback - 20%	10	137	<b>0.2</b>	15	0.3	0	0	0	0
Sc.1 – Positive feedback + 20%	10	137	<b>0.3</b>	15	0.3	0	0	0	0
Sc.1 – Dominance value - 20%	10	137	0.25	<b>12</b>	0.3	0	0	0	0
Sc.1 – Dominance value + 20%	10	137	0.25	<b>18</b>	0.3	0	0	0	0
Sc.1 – Compete threshold - 20%	10	137	0.25	15	<b>0.24</b>	0	0	0	0
Sc.1 – Compete threshold + 20%	10	137	0.25	15	<b>0.36</b>	0	0	0	0
Sc.6 – Mean body protein dep. - 50%	10	137	0.25	15	0.3	<b>5</b>	10	30	30
Sc.6 – Mean body protein dep. + 50%	10	137	0.25	15	0.3	<b>15</b>	10	30	30
Sc.6 – Positive feedback - 50%	10	137	0.25	15	0.3	30	<b>15</b>	30	30
Sc.6 – Positive feedback + 50%	10	137	0.25	15	0.3	30	<b>45</b>	30	30
Sc.6 – Dominance value - 50%	10	137	0.25	15	0.3	30	10	<b>15</b>	30
Sc.6 – Dominance value + 50%	10	137	0.25	15	0.3	30	10	<b>45</b>	30
Sc.6 – Compete threshold - 50%	10	137	0.25	15	0.3	30	10	30	<b>15</b>
Sc.6 – Compete threshold + 50%	10	137	0.25	15	0.3	30	10	30	<b>45</b>
Sc.6 – Group size - 50%	<b>15</b>	137	0.25	15	0.3	30	10	30	30
Sc.6 – Group size + 50%	<b>5</b>	137	0.25	15	0.3	30	10	30	30

Feeding, social interaction and growth patterns on individual and group level were obtained from day 4 to 14 in the model. Feeding patterns were: feed intake (g/day), feeding time (min/day), feeding rate (g/min/day), meal frequency (no./day and no./hour), meal duration (min/meal/day), and meal size (g/meal/day). Social interaction patterns were: conflicts (no./day), avoidings (no./day), successful displacements attempts (no./day), unsuccessful displacement attempts (no./day), successful displacement resists (no./day) and displacements (no./day). Growth patterns were: body weight (kg) and body weight gain (g/day).



### 6.2.6 Statistical analysis

Statistical analysis was performed using SAS (version 9.3; SAS Institute Inc., Cary, NC, USA). Data were analysed using descriptive statistics and general linear models. Data were averaged over 11 days and analysed at pen level with a general linear model to test the effect of scenarios on feeding, social interaction and growth patterns. When scenarios appeared to be different ( $P < 0.05$ ) a post-hoc pairwise comparison was conducted with a LSD test.

In scenario 2 to 5, pigs in a pen were ranked and categorised per simulation based on their values for the four parameters *Mean body protein deposition*, *Positive feedback*, *Dominance value* and *Compete threshold*. The two pigs with the highest value were categorised as high, the two with the lowest value as low, and the remaining pigs were categorised as medium. The average for feeding, social interaction and growth patterns was taken per category and over days. Next, per scenario, high, medium and low ranking pigs were compared for feeding, social interaction and growth patterns using a general linear model. When patterns appeared to be different ( $P < 0.05$ ) a post-hoc pairwise comparison was conducted with a LSD test.

In scenario 6, pigs in a pen were ranked and categorised per simulation based on their averages for feeding, social interaction and growth patterns over 11 days. Two pigs with the lowest average and two pigs with the highest average were selected and respectively categorised based on their meal frequency (meal eater and nibbler), feeding rate (slow and fast eater), conflicts (few conflicts and many conflicts), percentage of displacement attempts to conflicts (avoider and approacher), received displacements received (being avoided and receiver), body weight gain (slow and fast grower). Remaining pigs were categorised as medium. The average for the four parameters *Mean body protein deposition*, *Positive feedback*, *Dominance value* and *Compete threshold* was taken per category. Next, per pattern, high, medium and low ranking pigs were compared for averages of *Mean body protein deposition*, *Positive feedback*, *Dominance value* and *Compete threshold* using a general linear model. When patterns appeared to be different ( $P < 0.05$ ) a post-hoc pairwise comparison was conducted with a LSD test.

## 6.3 Results

### 6.3.1 Daily feeding, social interaction and growth patterns at group level

Mean group patterns of feed intake, feeding time, feeding rate and body weight were similar in all six scenarios (Table 4). Meal patterns differed between scenarios: meal frequency was highest in scenario 1, 2 and 3, and lowest in scenario 4 and 6, whereas meal duration and meal size had opposite results. Also mean social interaction patterns differed between scenarios: conflicts and displacement attempts (successful

and unsuccessful) were highest in scenario 1, 2 and 3, and lowest in scenario 4 and 6. The number of avoidings was lowest in scenario 1, 2, 3 and 5 and highest in scenario 6. Body weight and body weight gain was similar in all six scenarios.

**Table 4.** Mean  $\pm$ SD of feeding, social interaction and growth patterns at pen level for six scenarios and the *P*-value for differences between scenarios.\*

	1. No variation	2. Growth potential	3. Meal type	4. Dominance	5. Coping style	6. Combined variation	<i>P</i> - <i>value</i>
<i>Feeding patterns</i>							
Feed intake (g/day)	1672 $\pm$ 2	1671 $\pm$ 5	1671 $\pm$ 9	1674 $\pm$ 2	1673 $\pm$ 3	1672 $\pm$ 10	0.293
Feeding time (min/day)	83.7 $\pm$ 0.1	83.7 $\pm$ 0.1	83.6 $\pm$ 0.5	83.8 $\pm$ 0.1	83.7 $\pm$ 0.1	83.7 $\pm$ 0.5	0.221
Feeding rate (g/min/day)	20.0 $\pm$ 0.0	20.0 $\pm$ 0.1	20.0 $\pm$ 0.0	20.0 $\pm$ 0.0	20.0 $\pm$ 0.0	20.0 $\pm$ 0.1	0.287
Meal frequency (no./day)	20.7 $\pm$ 0.3 <sup>a</sup>	20.8 $\pm$ 0.4 <sup>a</sup>	21.1 $\pm$ 0.8 <sup>a</sup>	18.1 $\pm$ 1.0 <sup>b</sup>	19.4 $\pm$ 1.7 <sup>c</sup>	18.2 $\pm$ 1.8 <sup>b</sup>	<0.001
Meal duration (min/meal/day)	4.2 $\pm$ 0.1 <sup>a</sup>	4.2 $\pm$ 0.1 <sup>a</sup>	4.2 $\pm$ 0.2 <sup>a</sup>	4.8 $\pm$ 0.3 <sup>b</sup>	4.5 $\pm$ 0.4 <sup>c</sup>	4.9 $\pm$ 0.5 <sup>b</sup>	<0.001
Meal size (g/meal/day)	85.0 $\pm$ 1.5 <sup>a</sup>	84.4 $\pm$ 1.6 <sup>a</sup>	83.7 $\pm$ 3.5 <sup>a</sup>	97.1 $\pm$ 5.2 <sup>b</sup>	89.6 $\pm$ 7.4 <sup>c</sup>	97.8 $\pm$ 8.9 <sup>b</sup>	<0.001
<i>Social interaction patterns</i>							
Conflicts (no./day)	130 $\pm$ 3 <sup>a</sup>	130 $\pm$ 3 <sup>ab</sup>	132 $\pm$ 5 <sup>b</sup>	126 $\pm$ 5 <sup>c</sup>	128 $\pm$ 3 <sup>d</sup>	128 $\pm$ 6 <sup>d</sup>	<0.001
Avoidings (no./day)	102 $\pm$ 2 <sup>a</sup>	102 $\pm$ 3 <sup>a</sup>	103 $\pm$ 4 <sup>a</sup>	105 $\pm$ 3 <sup>b</sup>	103 $\pm$ 5 <sup>a</sup>	108 $\pm$ 6 <sup>c</sup>	<0.001
Displacement attempts							
Successful (no./day)	13.8 $\pm$ 0.4 <sup>a</sup>	13.9 $\pm$ 0.9 <sup>a</sup>	14.0 $\pm$ 0.5 <sup>a</sup>	10.5 $\pm$ 1.3 <sup>b</sup>	12.3 $\pm$ 1.9 <sup>c</sup>	10.2 $\pm$ 1.9 <sup>b</sup>	<0.001
Unsuccessful (no./day)	13.9 $\pm$ 0.5 <sup>a</sup>	13.9 $\pm$ 1.6 <sup>a</sup>	14.2 $\pm$ 0.6 <sup>a</sup>	9.8 $\pm$ 1.9 <sup>b</sup>	12.4 $\pm$ 1.9 <sup>c</sup>	9.7 $\pm$ 2.5 <sup>b</sup>	<0.001
<i>Growth patterns</i>							
Body weight (kg)	34.9 $\pm$ 0.0	34.8 $\pm$ 0.2	34.8 $\pm$ 0.0	34.9 $\pm$ 0.1	34.8 $\pm$ 0.0	34.8 $\pm$ 0.2	0.324
Body weight gain (g/day)	834 $\pm$ 1	831 $\pm$ 14	833 $\pm$ 5	834 $\pm$ 0.9	834 $\pm$ 0.9	830 $\pm$ 14	0.073

\* The *p*-value of significance levels based on 50 runs per scenario is given for the comparison between scenarios per pattern. Means with different superscripts within a row are significantly different.

### 6.3.2 The effect of variation in pig characteristics

Feeding, social interaction and growth patterns were compared between pigs that were categorised as low and high based on their values for the two parameters that are related to physiological factors: *Mean body protein deposition* and *Positive feedback* (Table 5). Pigs categorised with a low *Mean body protein deposition* (Low PD, mean: 119 g/day) had a significant lower feed intake, higher feeding time, lower feeding rate, lower meal size, lower body weight and lower body weight gain compared to pigs categorised as high body protein deposition potential (High PD, mean: 154 g/day). *Positive feedback* affected all patterns, except for successful resists. Pigs categorised with a low *Positive feedback* value (Low PF, mean: 0.15) had a lower feed intake, less feeding time, shorter meal duration, lower meal size, lower body weight, lower body

weight gain, and had a higher feeding rate, higher meal frequency, more conflicts, more avoidings and more (successful and unsuccessful) displacement attempts and displacements compared to pigs with a high *Positive feedback* value (High PF, mean: 0.35).

**Table 5.** Mean  $\pm$ SD of feeding, social interaction and growth patterns of pigs low or high in categories of *Mean body protein deposition* (PD) and *Positive feedback* (PF) (scenario 2 and 3) and the *P*-value for differences between scenarios. \*

	Scenario 2. Growth potential			Scenario 3. Meal type		
	Low PD	High PD	<i>P</i> -value	Low PF	High PF	<i>P</i> -value
<i>Feeding patterns</i>						
Feed intake (g/day)	1657 $\pm$ 9	1686 $\pm$ 8	<0.001	1641 $\pm$ 15	1703 $\pm$ 12	<0.001
Feeding time (min/day)	84.1 $\pm$ 0.3	83.3 $\pm$ 0.3	<0.001	81.8 $\pm$ 0.9	85.5 $\pm$ 0.7	<0.001
Feeding rate (g/min/day)	19.7 $\pm$ 0.1	20.3 $\pm$ 0.1	<0.001	20.1 $\pm$ 0.0	20.0 $\pm$ 0.1	<0.001
Meal frequency (no./day)	20.9 $\pm$ 0.6	20.7 $\pm$ 0.7	0.369	23.1 $\pm$ 1.6	19.5 $\pm$ 0.9	<0.001
Meal duration min/meal/day)	4.2 $\pm$ 0.1	4.2 $\pm$ 0.1	0.830	3.7 $\pm$ 0.3	4.6 $\pm$ 0.2	<0.001
Meal size (g/meal/day)	83.2 $\pm$ 2.7	85.4 $\pm$ 2.8	<0.001	74.0 $\pm$ 5.8	91.9 $\pm$ 4.7	<0.001
<i>Social interaction patterns</i>						
Conflicts (no./day)	132 $\pm$ 7	130 $\pm$ 8	0.092	142 $\pm$ 10	122 $\pm$ 6	<0.001
Avoidings (no./day)	104 $\pm$ 6	102 $\pm$ 6	0.062	112 $\pm$ 8	96 $\pm$ 5	<0.001
Displacement attempts						
Successful (no./day)	14.0 $\pm$ 0.6	13.8 $\pm$ 0.7	0.322	15.1 $\pm$ 1.0	13.1 $\pm$ 0.7	<0.001
Unsuccessful (no./day)	14.0 $\pm$ 1.0	14.1 $\pm$ 1.3	0.590	15.2 $\pm$ 1.3	13.2 $\pm$ 1.1	<0.001
Receiving displacements						
Successful resists (no./day)	14.0 $\pm$ 0.9	14.0 $\pm$ 0.8	0.782	14.1 $\pm$ 1.0	14.3 $\pm$ 1.3	0.792
Displacements (no./day)	14.0 $\pm$ 0.7	13.9 $\pm$ 0.7	0.637	14.1 $\pm$ 1.0	13.7 $\pm$ 0.9	0.008
<i>Growth patterns</i>						
Body weight (kg)	34.1 $\pm$ 0.3	35.5 $\pm$ 0.3	<0.001	34.7 $\pm$ 0.1	35.0 $\pm$ 0.0	<0.001
Body weight gain (g/day)	782 $\pm$ 23	877 $\pm$ 17	<0.001	815 $\pm$ 8	851 $\pm$ 6	<0.001

\* The *p*-value of significance levels based on 50 runs per scenario is given for the comparison between pig categories per pattern and scenario, or if significant, the *p*-value of the pairwise comparison between the high and low category is given.

**Table 6.** Mean  $\pm$ SD of feeding, social interaction and growth patterns of pigs low or high in categories of *Dominance value* (DOM) and *Compete threshold* (COMP) (scenario 4 and 5) and the *P*-value for differences between scenarios.\*

	Scenario 4. Dominance			Scenario 5. Coping style		
	Low DOM	High DOM	<i>P-value</i>	Low COMP	High COMP	<i>P-value</i>
<i>Feeding patterns</i>						
Feed intake (g/day)	1600 ±27	1714 ±9	<0.001	1690 ±9	1648 ±12	<0.001
Feeding time (min/day)	79.7 ±1.4	86.1 ±0.5	<0.001	84.7 ±0.4	82.2 ±0.7	<0.001
Feeding rate (g/min/day)	20.1 ±0.0	19.9 ±0.0	<0.001	20.0 ±0.0	20.1 ±0.0	<0.001
Meal frequency (no./day)	21.6 ±0.9	15.4 ±1.0	<0.001	20.4 ±1.7	18.1 ±2.0	<0.001
Meal duration (min/meal/day)	3.8 ±0.1	5.7 ±0.4	<0.001	4.3 ±0.4	4.7 ±0.5	<0.001
Meal size (g/meal/day)	77.1 ±2.7	113.9 ±7.3	<0.001	86.7 ±7.0	95.5 ±9.3	<0.001
<i>Social interaction patterns</i>						
Conflicts (no./day)	249 ±35	59 ±9	<0.001	90 ±10	182 ±19	<0.001
Avoidings (no./day)	228 ±41	42 ±8	<0.001	61 ±8	164 ±24	<0.001
Displacement attempts						
Successful (no./day)	9.0 ±2.8	10.4 ±0.8	<0.001	14.7 ±1.7	8.9 ±3.0	<0.001
Unsuccessful (no./day)	11.7 ±3.9	7.0 ±1.2	<0.001	14.9 ±1.9	8.8 ±3.0	<0.001
Receiving displacements						
Successful resists (no./day)	10.6 ±2.3	7.4 ±1.9	<0.001	12.8 ±2.0	11.8 ±2.0	0.058
Displacements (no./day)	16.4 ±0.9	5.6 ±1.7	<0.001	12.7 ±2.0	11.6 ±2.0	0.008
<i>Growth patterns</i>						
Body weight (kg)	34.6 ±0.2	35.0 ± 0.0	<0.001	34.9 ±0.0	34.8 ±0.1	<0.001
Body weight gain (g/day)	807 ±17	851 ±3.5	<0.001	841 ±4	824 ±7	<0.001

\* The *p*-value of significance levels based on 50 runs per scenario is given for the comparison between pig categories per pattern and scenario, or if significant, the *p*-value of the pairwise comparison between the high and low category is given.

Feeding, social interaction and growth patterns were compared between pigs that were categorised as low or high based on their values for the two parameters that are related to the behavioural strategies: *Dominance value* and *Compete threshold* (Table 6). Pigs categorised as low social rank (Low DOM, mean: 9.0) had a lower feed intake, lower feeding time, shorter meal duration, lower meal size, lower body weight, less successful displacement attempts, lower body weight gain, and had a higher feeding

rate, meal frequency, more conflicts, more avoidings, more unsuccessful displacement attempts and more received displacements than pigs categorised as high social rank (High pigs, mean: 20.7). Pigs categorised with a passive coping style (high COMP, mean: 0.42) had, comparable to low ranking pigs, a lower feed intake, lower feeding time, higher feeding rate, lower body weight (gain), more conflicts, more avoidings and less successful displacement attempts than pigs with an active coping style (low COMP, mean: 0.18). Passive copers, however, in contrast to low ranking pigs, had fewer, longer and larger meals, and had less unsuccessful displacement attempts and received less (un)successful displacements than active copers.

### **6.3.3 Categorisation of pigs in feeding, social interaction and growth patterns**

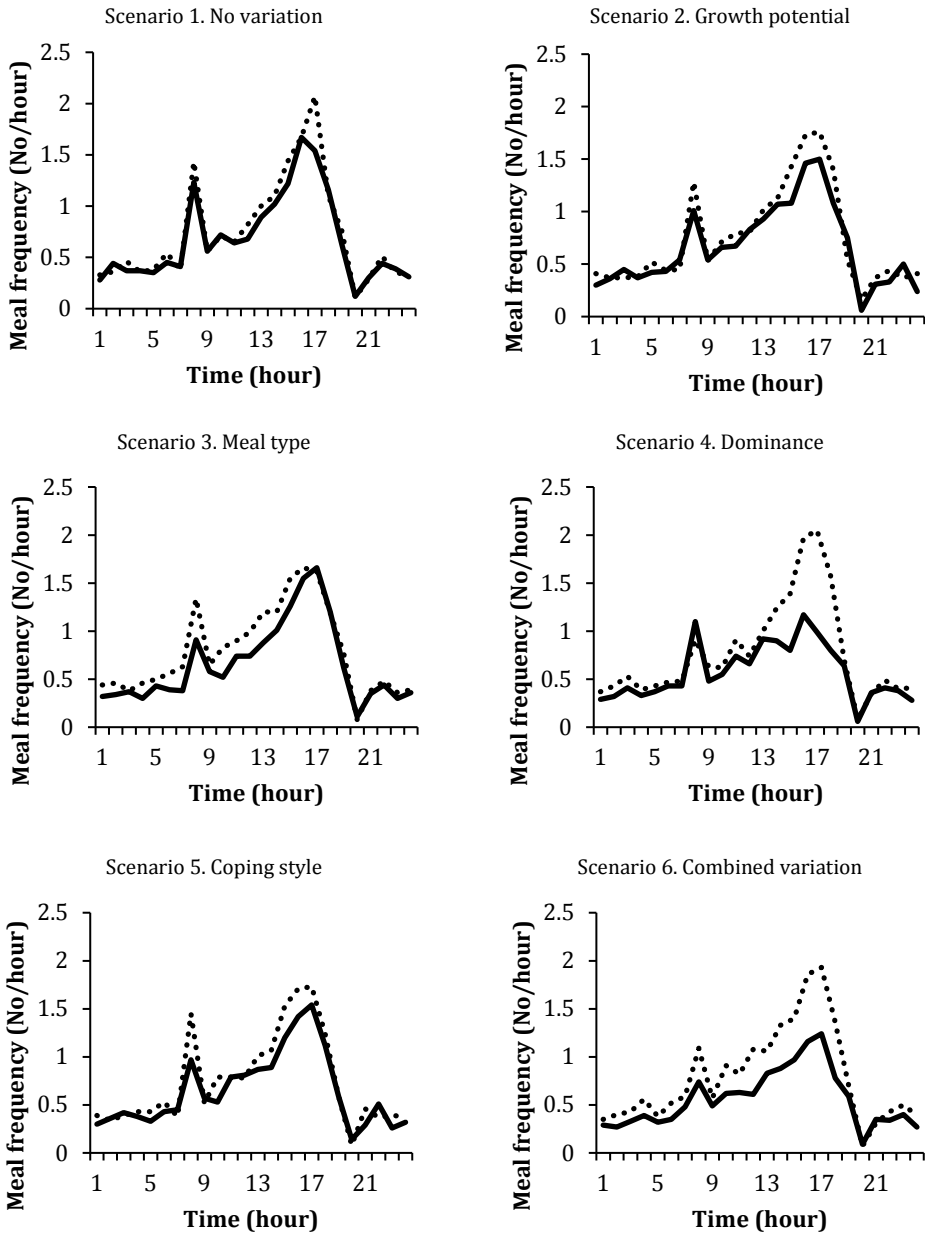
Pig characteristics (based on the four varied parameters) were compared between various categories in feeding, social interaction and growth patterns in scenario 6 (Table 7). Nibblers (22.3 meals/day) differed significantly from meal eaters (14.7 meals/day) with a lower value for *Positive feedback*, *Dominance value* and *Compete threshold*. Slow eaters (19.8 g/min/day) had a significantly lower *Mean body protein deposition*, lower *Compete threshold* and higher *Positive feedback* than fast eaters (20.2 g/min/day). Pigs with relatively few conflicts (56 conflicts/day) had a higher *Positive feedback*, higher *Dominance value* and lower *Compete threshold* value than pigs with relatively many conflicts (254 conflicts/day). Avoiders (approached 7% of conflicts) were less dominant and had a higher *Compete threshold* than approachers (approached 36% of conflicts). Receivers of displacement attempts (27 displacement attempts/day) were less dominant and had a lower *Compete threshold* than pigs that were being avoided (received 13 displacement attempts/day). Losers (lost 61% of interactions) had a lower *Dominance value* than winners (lost 40% of interactions). Slow growers (776 g/day) differed from fast growers (885 g/day) in all four parameters: a lower *Mean body protein deposition*, *Positive feedback* and *Dominance value* and higher *Compete threshold*.

**Table 7.** Mean  $\pm$ SD of parameters values related to pig categories in feeding, social interaction and growth patterns in scenario 6 and the  $P$ -value for differences between low and high pigs in various categories.\*

	Physiological factors				Behavioural strategies			
	Mean body protein deposition	<i>P</i> -value	Positive feedback	<i>P</i> -value	Dominance value	<i>P</i> -value	Compete threshold	<i>P</i> -value
<i>Feeding patterns</i>								
Nibbler	138 ±13	0.276	0.22 ±0.08	<0.001	10.5 ±3.8	<0.001	0.25 ±0.08	<0.001
Meal eater	138 ±14		0.31 ±0.06		18.6 ±3.5		0.34 ±0.10	
Slow eater	126 ±12	<0.001	0.28 ±0.08	<0.001	13.6 ±4.0	0.258	0.27 ±0.08	<0.001
Fast eater	147 ±11		0.22 ±0.08		14.3 ±5.1		0.33 ±0.10	
<i>Social interaction patterns</i>								
Few conflicts	135 ±15	0.352	0.27 ±0.07	0.093	19.6 ±3.1	<0.001	0.24 ±0.08	<0.001
Many conflicts	138 ±13		0.25 ±0.06		9.4 ±3.1		0.35 ±0.10	
Avoider	138 ±14	0.359	0.25 ±0.07	0.820	10.5 ±3.8	<0.001	0.38 ±0.09	<0.001
Approacher	135 ±14		0.26 ±0.08		18.3 ±3.9		0.20 ±0.07	
Receiver	138 ±13	0.481	0.26 ±0.07	0.662	9.7 ±2.9	<0.001	0.27 ±0.09	0.001
Being avoided	136 ±14		0.26 ±0.08		20.1 ±3.0		0.31 ±0.09	
Loser	140 ±13	0.174	0.24 ±0.07	0.405	9.0 ±2.6	<0.001	0.29 ±0.10	0.719
Winner	137 ±15		0.26 ±0.07		19.8 ±3.0		0.30 ±0.10	
<i>Growth patterns</i>								
Slow grower	123 ±11	<0.001	0.22 ±0.07	<0.001	12.5 ±4.6	<0.001	0.31 ±0.10	0.015
Fast grower	152 ±9		0.29 ±0.07		16.3 ±3.9		0.28 ±0.10	

\* The  $p$ -value of significance levels based on 50 runs per scenario is given for the comparison between all pig categories and if significant the  $p$ -value between the extreme categories in the pairwise comparison is given.

The distribution of meal frequency over 24 hours varied between the scenarios for pigs with a low (meal eater) and high meal frequency (nibbler) (Figure 1). The morning peak between meal eaters and nibblers differed most when *Positive feedback* (Scenario 3), *Compete threshold* (Scenario 5) and all four parameters (Scenario 6) were varied. The afternoon peak between meal eaters and nibblers differed most when *Dominance value* was varied (Scenario 4) and all four parameters (Scenario 6) were varied.



**Figure 1.** Hourly mean meal frequency on day 14 for pigs with a daily low (meal eater; —) and high meal frequency (Nibbler; ..... ) per day.

### 6.3.4 Sensitivity analysis

Variation by 20% in the value level of the four parameters (*Mean body protein deposition*, *Positive feedback*, *Dominance value* and *Compete threshold*) had limited effect (<20%) on most model results (Appendix I, Table A1). An exception was *Compete threshold*, of which an increase resulted in a decrease of displacement patterns (successful and unsuccessful displacement attempts, successful resists and displacements) by 26% and a decrease increased these patterns by 24%.

Variation among individuals with 50% in parameter values for the four parameters affected the mean values and standard deviation with less than 50% change, whereas variation in group size had an impact on feeding, social interaction and growth patterns of more than 50% change (Appendix I, Table A2). Increased group size affected mean values and standard deviation of meal frequency and all social interaction patterns, and standard deviation of feeding time and body weight gain. Decreased group size mainly affected the mean values and standard deviation of social interaction patterns.

## 6.4 Discussion

The aim of this study was to unravel causation of variation in feeding, social interaction and growth patterns among pigs. We used an ABM to explore the effects of physiological factors and behavioural strategies on behavioural patterns of group-housed pigs. We hypothesised that interaction between physiological factors and behavioural strategies of individuals might affect variation in feeding, social interaction and growth patterns among pigs and can explain the contrasting results in empirical studies.

Model results showed that variation in feeding, social interaction and growth patterns among pigs is caused partly by chance, from time effects and coincidence of conflicts. In Scenario 1, all pigs were identical for the parameters *Mean body protein deposition*, *Positive feedback*, *Dominance value* and *Compete threshold*, but they varied in feeding, social interaction and growth patterns. Variation in initial values of motivations for feeding, drinking, exploring and lying at the start of simulations explains these results, but variation can also be partly explained by coincidental conflicts at the feeder.

In real life, pigs can be expected to vary in characteristics that will affect physiological factors and behavioural strategies. When applied to this model, results showed that variation in *Mean body protein deposition*, which represented variation in growth capacity, mainly affected feed intake, feeding time, feeding rate, meal size and body weight (gain) of pigs, and partly explained variation in slow and fast eaters and growers (Table 5 and 7). This is in line with empirical results, in which Landrace and Large White pigs were fast eaters and also had a higher daily feed intake and body



weight gain than Pietrain pigs, which were slow eaters (Fernández et al., 2011). In that same study, Duroc pigs, who similarly to Landrace and Large White pigs had a higher growth potential, appeared slow eaters. These Duroc pigs, however, had the highest meal duration of the four breeds, which was strongly related with feeding rate (Fernández et al., 2011). This is in line with the model results, in which a higher positive feedback is associated with a higher meal size, a higher daily feed intake, a higher body weight gain and a lower feeding rate (Table 5). This suggests that differences in feeding, social interaction and growth patterns between these breeds can be explained by pig characteristics that affect variation in growth potential and meal duration.

Positive feedback in the model represented a reinforcement effect of feeding that affects meal duration and can be related to, for example, capacity of the stomach and signalling of stomach load. Model results showed that variation in *Positive feedback* affected all feeding and growth patterns in pigs, as well as almost all social interaction patterns (Table 5). A high positive feedback was associated with a higher daily feed intake, eating few but longer meals (meal eater) and fast grower. This is in line with multiple empirical studies, which found an association between increased daily feed intake, large meals, a high feeding rate and daily body weight gain (e.g. De Haer et al., 1993; Fernández et al., 2011; Labroue et al., 1997). Fernández et al. (2011) suggested that pigs with a meal eater and fast eater strategy have a higher productivity. Our study shows how this can be a result of positive feedback that stimulates longer meals.

Contrasting empirical results were found in the study by Nielsen et al. (1996a), where meal eaters had a lower feed intake and comparable body weight gain to nibblers. These results were comparable to our results in scenario 5, with a variation in *Compete threshold*. In this scenario, meal eaters were pigs with a passive coping style that had a lower feed intake, feeding time, and slightly lower body weight gain than nibblers (for example, see comparison of contrasting patterns between scenario 5 and 6 in Appendix II, Table A3). Since these model patterns were consistent with the empirical results of Nielsen et al. (1996a), this suggests that meal eaters in the empirical study were pigs with a passive coping style. This is also supported by the hourly patterns of meal frequency, in which a smaller morning peak for meal eater pigs in scenario 5 is in line with empirical results of Nielsen et al. (1996a), where pigs had no peak in meal frequency in the morning. Meal eater pigs in that study were suggested to have a disadvantageous feeding strategy. Our results, however, suggest that these pigs might have been pigs with similar feeding strategies (physiological factors), but they might have experienced more social constraints than other group mates due to their passive coping style.

Daily feed intake, feeding rate and meal patterns have been suggested to indicate social constraints inhibiting pigs within a group from feeding when they want to. Daily

feed intake and body weight gain, for example, decreased as group size increased (Hyun & Ellis, 2001). Pigs that experience social constraints can adapt to these constraints by changing their feeding patterns. If pigs are not able to adapt, however, they might have had limited access to the feeder and, therefore, show a decreased feed intake and body weight gain in comparison to group mates that have similar feed intake requirements and growth potential. A low feed intake and body weight gain, however, can also be associated with other factors, such as a low growth potential (Table 5). Therefore, interpretation of daily feed intake at individual level should be done cautiously. The same caution applies to the use of feeding rate as an indicator of social constraints at individual level. Feeding rate increases in larger group sizes and has been suggested to reflect the social constraints within a group (Boumans et al., 2017a; Nielsen, 1999). Our results suggest that feeding rate might not be a suitable indicator at individual level, because it is not only affected by social constraints. Results of slow versus fast eaters in scenario 6 showed that fast eaters were mainly pigs with a high growth potential, low positive feedback and passive coping style (Table 7). Although a low positive feedback and passive coping style are indeed associated with a lower feed intake and daily body weight gain (Table 5 and 6), this is in contrast to a higher growth potential, which had the largest impact on variation in feeding rate and is associated with a higher feed intake and body weight gain (Table 5). Thus feeding rate at individual level might also reflect a higher growth potential of pigs and not necessarily indicate social constraints.

A change in daily meal frequency at group level has also been suggested to be related to social constraints in group-housed pigs, in which an increased meal frequency can indicate increased aggression between pigs and a decreased meal frequency can indicate avoidance behaviour (Boumans et al., 2017a). Although daily meal frequency seems to be a good indicator for social constraints at group level, our results suggest that it might not be a suitable indicator at individual level. As shown in Appendix II and discussed above, a low meal frequency (meal eater pattern) at individual level can be associated with either a high or low feed intake. Therefore, interpretation of meal frequency at individual level should also be done cautiously. This suggests that feeding patterns, such as daily feed intake, meal frequency and feeding rate, by itself might not be good indicators at individual level.

A combination of feeding patterns might be needed to measure social constraints at individual level. Our results suggest that a high growth potential is associated with a high feed intake and high feeding rate, and therefore, a combination of low daily feed intake and high feeding rate might indicate social constraints. Moreover, these patterns in combination with a low meal frequency might indicate social constraints for a passive copier, whereas these patterns in combination with a high meal frequency might indicate social constraints for a low ranking pig. A low ranking pig, however, shows a feeding pattern comparable to a pig with a low positive feedback. A high

afternoon peak in hourly meal frequency is associated with low ranking pigs and can help to differentiate between the effect of a social constraint for a low dominant pig or a physiological effect via a low positive feedback.

Model results showed that variation in *Dominance value* affected all feeding, social interaction and growth patterns (Table 6). Classification in low and high ranking pigs showed that high ranking pigs were mostly meal eaters, whereas low ranking pigs were mostly nibblers. This is in line with empirical results of the study of Hoy et al. (2012). In their study, however, high ranking pigs also had more wins at the feeder than low ranking pigs (respectively 10.3 and 6.9 wins per day at the beginning of the growing period), which slightly differs from our results, in which low ranking pigs had mostly comparable or more wins than high ranking pigs. This might be explained by the assumed hierarchy distribution. Simulated pigs might more easily approach higher ranking pigs than real-life pigs, because of the simplified linear and fixed hierarchy distribution or the effect of probability in decisions to avoid or approach feeding pigs. Especially in the simulated period of the first two weeks, when pigs have a longer daily feeding time and thus more competition, lower ranked pigs are more likely to approach higher ranked pigs.

In the empirical study of Leiber-Schotte (2009), where subordinate boars had fewer and longer meals than dominant boars, pigs were fed with electronic feeding stations with protected sides and a rear door that was automatically closed during feeding, protecting feeding pigs from being displaced. Although we did not simulate such a feeder, the current results suggest that without displacement possibilities, pigs in group-housing will perform longer meals than usual. This can cause more waiting behaviour for the feeder, in which especially subordinate pigs might have to wait longer, which increases their hunger and motivation for longer meals when they can feed. And since they cannot be displaced from the feeder, it can be expected that once they have reached the feeder, they will perform fewer but longer meals to reach their daily feed intake.

The average number of conflicts and displacement attempts within a group was lowest when variation in *Dominance value* among pigs was simulated (Table 4). The effect of variation in dominance was expected to reduce aggression, since the dominance order describes the predictable relationship and avoidance order between animals that likely reduces aggression with a more clear dominance order (Lindberg, 2001). Also, variation between pigs in *Compete threshold*, which represented variation in coping style, decreased average displacement attempts within a group (Table 4). The beneficial effect of variation in coping style within group-housed pigs was also shown in an empirical study with homogenous groups of pigs (with either all an active or passive coping style) or heterogeneous groups of pigs having either an active or passive coping style (Hessing et al., 1994). Agonistic behaviour shortly after mixing

was higher in the homogeneous groups consisting of pigs with only active coping styles, than in the other two group types. Furthermore, the mean daily body weight gain was lower in the homogeneous groups consisting of only active copers or only passive copers. This decreased growth is inconsistent with our model results, in which body weight gain was similar between all scenarios. This inconsistency can be explained by the prevalence of health problems in the empirical pigs, which decreased growth especially in the homogeneous groups.

This study contributes to understanding individual variation and can be used to better understand the capacity of animals to cope with environmental factors and their susceptibility to stressors. Feeding patterns in pigs have been found to be consistent over time and flexible when exposed to social competitive situations, however, with variation in coping ability among individuals (Bornett et al., 2000b). Our results show how pig characteristics that affect physiological factors and behavioural strategies can affect the ability of pigs to cope with social constraints. Due to dominance rank, for example, pigs can become meal eaters or nibblers, which can affect their feed intake and aggressive interactions during social constraints.

To conclude, this study increased understanding of the causation of variation in feeding, social interaction and growth patterns among group-housed pigs. Individual variation in these patterns resulted partly from time effects and coincidence in conflicts, and partly from differences in pig characteristics of growth potential, positive feedback, dominance, and coping style. Variation between meal eaters and nibblers, and between slow and fast eaters, can be explained by pig characteristics that both affect physiological factors and behavioural strategies. Individual variation in behavioural strategies can reduce aggression at group level, but can also make some animals more susceptible to social constraints, especially low-ranking pigs and pigs with a passive coping style. Variation in feeding patterns can be an indication of social constraints. A combination of feeding patterns, such as a decreased feed intake, an increased feeding rate, and an increased or decreased meal frequency, might be suitable for identifying individuals that experience social constraints.

### **Acknowledgements**

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## Appendix I. Sensitivity analysis of parameter values

**Table A1.** Mean values  $\pm$  SD of feeding, social interaction and growth patterns in the sensitivity analysis in scenario 1 (all individuals similar parameter values).

Pattern	Sc.1. No variation	Mean body protein dep. +20%	Mean body protein dep. -20%	Positive feedback + 20%	Positive feedback - 20%	Dominance value + 20%	Dominance value - 20%	Compete threshold + 20%	Compete threshold - 20%
<i>Feeding patterns</i>									
Feed intake (g/day)	1672 $\pm 2$	1697 $\pm 2$	1646 $\pm 2$	1690 $\pm 2$	1655 $\pm 2$	1673 $\pm 2$	1673 $\pm 2$	1675 $\pm 2$	1672 $\pm 2$
Feeding time (min/day)	83.7 $\pm 0.1$	83.3 $\pm 0.1$	84.1 $\pm 0.1$	84.7 $\pm 0.1$	82.7 $\pm 0.1$	83.7 $\pm 0.1$	83.7 $\pm 0.1$	83.8 $\pm 0.1$	83.6 $\pm 0.1$
Feeding rate (g/min/day)	20.0 $\pm 0.0$	20.4 $\pm 0.0$	19.6 $\pm 0.0$	20.0 $\pm 0.0$	20.1 $\pm 0.0$	20.0 $\pm 0.0$	20.0 $\pm 0.0$	20.0 $\pm 0.0$	20.0 $\pm 0.0$
Meal frequency (no./day)	20.7 $\pm 0.3$	19.6 $\pm 0.4$	21.7 $\pm 0.5$	19.5 $\pm 0.4$	22.0 $\pm 0.4$	20.6 $\pm 0.4$	20.5 $\pm 0.4$	17.5 $\pm 0.3$	23.7 $\pm 0.6^s$
Meal duration (min/meal/day)	4.2 $\pm 0.1$	4.4 $\pm 0.1$	4.0 $\pm 0.1$	4.5 $\pm 0.1$	3.9 $\pm 0.1$	4.2 $\pm 0.1$	4.2 $\pm 0.1$	4.9 $\pm 0.1$	3.7 $\pm 0.1$
Meal size (g/meal/day)	85.0 $\pm 1.5$	90.3 $\pm 1.7$	79.6 $\pm 1.7$	91.0 $\pm 1.8$	78.7 $\pm 1.4$	85.2 $\pm 1.5$	85.4 $\pm 1.8$	99.2 $\pm 1.6$	74.8 $\pm 1.6$
<i>Social interaction patterns</i>									
Conflicts (no./day)	130 $\pm 3$	119 $\pm 3$	141 $\pm 3$	123 $\pm 3$	136 $\pm 3$	129 $\pm 3$	129 $\pm 3$	133 $\pm 3$	126 $\pm 3$
Avoidings (No./day)	102 $\pm 2$	93 $\pm 2$	111 $\pm 2$	97 $\pm 2$	108 $\pm 2$	102 $\pm 2$	102 $\pm 2$	112 $\pm 2$	92 $\pm 2$
Displacement attempts									
Successful (no./day)	13.8 $\pm 0.4$	12.6 $\pm 0.4$	15.0 $\pm 0.5$	13.1 $\pm 0.5$	14.4 $\pm 0.4$	13.7 $\pm 0.4$	13.7 $\pm 0.5$	10.2 <sup>m</sup> $\pm 0.3$	17.1 <sup>m</sup> $\pm 0.6^s$
Unsuccessful (no./day)	13.9 $\pm 0.5$	12.7 $\pm 0.5$	15.2 $\pm 0.6$	13.3 $\pm 0.4$	14.7 $\pm 0.4$	13.9 $\pm 0.4$	13.9 $\pm 0.5$	10.3 <sup>m</sup> $\pm 0.4$	17.3 <sup>m</sup> $\pm 0.6$
<i>Growth patterns</i>									
Body weight (kg)	34.9 $\pm 0.0$	35.8 $\pm 0.0$	33.8 $\pm 0.0$	34.9 0.0	34.8 $\pm 0.0$	34.9 $\pm 0.0$	34.9 $\pm 0.0$	34.9 $\pm 0.0$	34.9 $\pm 0.0$
Body weight gain (g/day)	834 $\pm 3$	902 $\pm 1$	754 $\pm 1$	843 $\pm 1$	824 $\pm 1$	834 $\pm 1$	834 $\pm 1$	835 $\pm 1$	834 $\pm 3$

<sup>m</sup> More than 20% change in mean values, <sup>s</sup> More than 20% change in SD

**Table A2.** Mean values  $\pm$  SD of feeding, social interaction and growth patterns in the sensitivity analysis in scenario 6 (all parameter values varied among individuals).

	Sc.6. Combined variation	Mean body protein dep. +50%	Mean body protein dep. -50%	Positive feedback + 50%	Positive feedback - 50%	Dominance value + 50%	Dominance value - 50%	Compete threshold + 50%	Compete threshold - 50%	Group size + 50%	Group size - 50%
<i>Feeding patterns</i>											
Feed intake (g/day)	1672 $\pm 10$	1670 $\pm 10$	1674 $\pm 10$	1670 $\pm 11$	1674 $\pm 7$	1672 $\pm 12$	1673 $\pm 11$	1672 $\pm 11$	1671 $\pm 11$	1560 $\pm 8$	1699 $\pm 16^s$
Feeding time (min/day)	83.7 $\pm 0.5$	83.6 $\pm 0.5$	83.8 $\pm 0.5$	83.6 $\pm 0.6$	83.8 $\pm 0.3$	83.7 $\pm 0.6$	83.8 $\pm 0.6$	83.7 $\pm 0.6$	83.6 $\pm 0.5$	71.1 $\pm 0.3$	97.0 $\pm 1.0$
Feeding rate (g/min/day)	20.0 $\pm 0.1$	20.0 $\pm 0.1$	20.0 $\pm 0.0$	20.0 $\pm 0.1$	20.0 $\pm 0.1$	20.0 $\pm 0.1$	20.0 $\pm 0.1$	20.0 $\pm 0.1$	20.0 $\pm 0.1$	21.9 $\pm 0.1$	17.6 $\pm 0.1$
Meal frequency (no./day)	18.2 $\pm 1.8$	18.3 $\pm 1.5$	18.3 $\pm 1.6$	18.7 $\pm 1.8$	17.8 $\pm 1.6$	17.5 $\pm 1.5$	19.0 $\pm 1.6$	18.2 $\pm 2.0$	18.9 $\pm 1.6$	31.4 <sup>m</sup> $\pm 4.8^s$	15.6 $\pm 1.3$
Meal duration (min/meal/day)	4.9 $\pm 0.5$	4.8 $\pm 0.4$	4.9 $\pm 0.4$	4.8 $\pm 0.5$	4.9 $\pm 0.4$	5.1 $\pm 0.5$	4.6 $\pm 0.4$	4.9 $\pm 0.5$	4.7 $\pm 0.4$	2.5 $\pm 0.4$	6.4 $\pm 0.5$
Meal size (g/meal/day)	97.8 $\pm 8.9$	97 $\pm 7.8$	98 $\pm 8.2$	96 $\pm 9.2$	99 $\pm 8.7$	102 $\pm 9.3$	93 $\pm 8.4$	98 $\pm 10.4$	94 $\pm 7.9$	55 $\pm 9.2$	112 $\pm 9.1$
<i>Social interaction Patterns</i>											
Conflicts (no./day)	128 $\pm 6$	129 $\pm 6$	129 $\pm 6$	131 $\pm 6$	126 $\pm 5$	126 $\pm 6$	129 $\pm 5$	128 $\pm 5$	129 $\pm 6$	305 <sup>m</sup> $\pm 16^s$	32 <sup>m</sup> $\pm 2^s$
Avoidings (No./day)	108 $\pm 6$	109 $\pm 7$	108 $\pm 6$	111 $\pm 7$	107 $\pm 6$	110 $\pm 5$	106 $\pm 5$	108 $\pm 7$	108 $\pm 5$	252 <sup>m</sup> $\pm 8$	27 <sup>m</sup> $\pm 3$
Displacement attempts											
Successful (no./day)	10.2 $\pm 1.9$	10.4 $\pm 1.8$	10.4 $\pm 1.8$	10.4 $\pm 2.1$	9.9 $\pm 1.9$	9.0 $\pm 1.7$	11.5 $\pm 1.7$	10.2 $\pm 2.3$	11.1 $\pm 1.7$	26.4 <sup>m</sup> $\pm 5.2^s$	2.9 <sup>m</sup> $\pm 0.6^s$
Unsuccessful (no./day)	9.7 $\pm 2.5$	9.9 $\pm 2.5$	10.1 $\pm 2.1$	9.9 $\pm 2.5$	9.3 $\pm 2.4$	7.3 $\pm 2.6$	11.5 $\pm 1.8$	10.0 $\pm 2.6$	10.6 $\pm 2.1$	27.2 <sup>m</sup> $\pm 5.6^s$	2.6 <sup>m</sup> $\pm 0.7^s$
<i>Growth patterns</i>											
Body weight (kg)	34.8 $\pm 0.2$	34.8 $\pm 0.2$	34.8 $\pm 0.1$	34.8 $\pm 0.2$	34.8 $\pm 0.2$	34.8 $\pm 0.2$	34.8 $\pm 0.2$	34.8 $\pm 0.2$	34.8 $\pm 0.2$	34.5 $\pm 0.1$	34.9 $\pm 0.3$
Body weight gain (g/day)	830 $\pm 14$	829 $\pm 16$	833 $\pm 8$	827 $\pm 13$	831 $\pm 15$	831 $\pm 13$	831 $\pm 12$	831 $\pm 12$	831 $\pm 15$	795 $\pm 10$	838 $\pm 19$

<sup>m</sup> More than 50% change in mean values, <sup>s</sup> More than 50% change in SD

## Appendix II. Feeding, social interaction and growth patterns of nibblers and meal eaters

**Table A3.** Mean  $\pm$  SD feeding, social interaction and growth patterns of low and high meal frequency pigs in scenario 5 and 6.\*

	Scenario 5 (Compete threshold varied)			Scenario 6 (All parameters varied)		
	Meal eater	Nibbler	P-value	Meal eater	Nibbler	P-value
<i>Feeding patterns</i>						
Feed intake (g/day)	1655 $\pm$ 14	1685 $\pm$ 8	<0.001	1719 $\pm$ 31	1625 $\pm$ 37	<0.001
Feeding time (min/day)	82.6 $\pm$ 0.8	84.4 $\pm$ 0.5	<0.001	86.3 $\pm$ 1.6	80.9 $\pm$ 2.0	<0.001
Feeding rate (g/min/day)	20.0 $\pm$ 0.1	20.0 $\pm$ 0.0	<0.001	19.9 $\pm$ 0.2	20.1 $\pm$ 0.2	<0.001
Meal frequency (no./day)	17.8 $\pm$ 1.8	20.9 $\pm$ 1.7	<0.001	14.7 $\pm$ 1.4	22.3 $\pm$ 2.6	<0.001
Meal duration (min/meal/day)	4.8 $\pm$ 0.4	4.2 $\pm$ 0.3	<0.001	6.0 $\pm$ 0.6	3.8 $\pm$ 0.4	<0.001
Meal size (g/meal/day)	97.3 $\pm$ 8.9	84.4 $\pm$ 6.7	<0.001	120.4 $\pm$ 12	76.8 $\pm$ 8.8	<0.001
<i>Social interaction patterns</i>						
Conflicts (no./day)	167 $\pm$ 25	103 $\pm$ 14	<0.001	79 $\pm$ 33	191 $\pm$ 59	<0.001
Avoidings (no./day)	148 $\pm$ 30	74 $\pm$ 14	<0.001	64 $\pm$ 34	164 $\pm$ 63	<0.001
Displacement attempts						
Successful (no./day)	9.1 $\pm$ 2.9	14.8 $\pm$ 1.7	<0.001	8.9 $\pm$ 1.7	11.6 $\pm$ 3.9	<0.001
Unsuccessful (no./day)	9.4 $\pm$ 3.2	14.6 $\pm$ 1.8	<0.001	6.5 $\pm$ 1.7	14.8 $\pm$ 6.3	<0.001
Receiving displacements						
Successful resists (no./day)	11.8 $\pm$ 2.1	12.6 $\pm$ 2.0	0.139	8.4 $\pm$ 2.7	10.7 $\pm$ 2.8	<0.001
Displacements (no./day)	11.1 $\pm$ 1.9	13.5 $\pm$ 2.1	<0.001	6.3 $\pm$ 2.1	15.1 $\pm$ 3.6	<0.001
<i>Growth patterns</i>						
Body weight (kg)	34.8 $\pm$ 0.1	34.9 $\pm$ 0.0	<0.001	35.0 $\pm$ 0.4	34.7 $\pm$ 0.4	<0.001
Body weight gain (g/day)	826 $\pm$ 6	839 $\pm$ 3	<0.001	855 $\pm$ 31	813 $\pm$ 27	<0.001

\* The *p*-value of significance levels based on 50 runs per scenario is given for the comparison between pig categories per pattern and scenario, or if significant, the *p*-value of the pairwise comparison between the high and low category is given.





# **Chapter 7**

## **General discussion**

## 7.1 Introduction

The transition towards sustainable pig production systems is receiving increasing attention nowadays. Sustainability, however, is a multidimensional concept that includes many environmental, economic and societal issues. This multidimensionality also implies that there is no unique, single solution to sustainability, because agro-ecological and socio-economic circumstances of pig production systems differ across regions (De Boer, 2012). In developed countries, for example, concerns exist about the welfare of our production animals. Welfare issues may lead to legal restrictions and are either positively or negatively related to other sustainability issues (Chemineau, 2016; Tucker et al., 2013). To be able to make conscious decisions for desired developments of pig production systems, we need to understand trade-offs and synergies between welfare and other sustainability issues. Pig behaviour plays a central role in sustainability, as it is an important indicator for pig welfare and can also affect other sustainability issues. Researchers have tried with empirical studies to understand behaviour, underlying motivations, and related welfare consequences, but so far have been unable to unravel the interaction between internal factors (i.e. from within the animal), external factors (i.e. from the environment of the animal) and behavioural motivations (Rushen & de Passillé, 2009).

Modelling studies can help in understanding relations between behaviour and welfare. So far, however, these studies focused on understanding animal behaviour and underlying motivations, or on evaluating or predicting animal welfare at farm level without understanding motivations underlying behaviour. The integration of both research domains is missing, although it is essential for understanding pig behaviour and related welfare. The challenge, therefore, is to integrate these two approaches in such a way that both underlying motivations and welfare as well as other sustainability issues related to a behaviour can be analysed. Agent-based models are especially suitable to study individual variation and interaction among individuals. These types of models have much potential for understanding animal behaviour and assessing animal welfare, but have been rarely used for this purpose (Asher et al., 2009).

The two aims of this thesis were: 1) to assess the use of agent-based modelling for understanding pig behaviour and underlying motivations, and 2) to apply agent-based modelling for increasing our understanding of pig behaviour, and related animal welfare and productivity performance. In line with the first aim, the use of agent-based modelling was explored with a case study of tail biting behaviour (Chapter 2). For the second aim, a more complex and in-depth model on feeding behaviour was built in three steps: first, the impact of internal (physiological) factors on feeding behaviour (Chapter 3); second, the impact of hormonal circadian rhythms on physiological factors (Chapter 4); third, the impact of interaction between internal and

external social factors on feeding behaviour (Chapter 5). Thereafter, the model was used to understand individual variation in pig behaviour and related behavioural and growth performance (Chapter 6).

In the next sections, results will be discussed in relation to these two aims. First, results related to whether agent-based modelling can be used to understand behaviour and motivation (paragraph 7.2); second, results related to the use of agent-based modelling for understanding animal welfare (paragraph 7.3); third, results related to the application of the developed model for sustainability analysis (paragraph 7.4), and methodological challenges of the applied method (paragraph 7.5). The final section presents main conclusions of this thesis (paragraph 7.6).

## **7.2 The use of agent-based modelling for understanding behaviour and underlying motivations**

Agent-based modelling of animal behaviour has been used mainly to study collective behaviour, such as in insect societies, fish schools, and groups of primates (Babin-Fenske & Anand, 2011; Bryson et al., 2007; Evers et al., 2014; Hemelrijk & Kunz, 2005; Kunz & Hemelrijk, 2003; Rangel-Huerta & Muñoz-Meléndez, 2010; Vanderelst et al., 2009). A few examples exist of agent-based models of behaviour of farm animals, such as laying hens and broiler chickens (e.g. Asher & Collins, 2012; Asher et al., 2013; Collins & Sumpter, 2007). One study was found that focused on social spatial behaviour in pigs (Stricklin et al., 1998; Stricklin et al., 1995). We explored the use of agent-based modelling for understanding pig behaviour with a case study of tail biting behaviour in pigs.

### **7.2.1 A case study in tail biting behaviour**

In pig production, tail biting behaviour is considered to be a major welfare issue with a large impact on the profitability of a farm (D'Eath et al., 2014; Schrøder-Petersen & Simonsen, 2001). Tail biting behaviour has been studied intensively (e.g. Bracke, 2009; D'Eath et al., 2014; Larsen et al., 2016; Munsterhjelm et al., 2013b; Taylor et al., 2012; Ursinus et al., 2014; Zonderland, 2010; Zupan et al., 2012). These studies have tried to explain the complex interaction between internal (e.g. genotype and sex) and external factors (e.g. diet and stocking density) underlying this behaviour, but were in most cases not able to elucidate the causation. Bracke et al. (2004a, 2004b) developed a decision support system to assess the risk for tail biting behaviour in commercial pig housing systems. Their model can predict the occurrence of tail biting behaviour in different housing conditions, but is unable to explore motivations underlying behaviour and to distinguish welfare of individual pigs. Other behaviour-related models for tail biting behaviour were not found at the start of this research.

The agent-based model developed to explore tail biting behaviour demonstrated its value for increasing our understanding of the behaviour and underlying motivation (Chapter 2). Model results show how redirected exploratory motivation in pigs that are unable to express exploration behaviour can cause the varying emergence of tail biting behaviour observed in barren housed pigs. Furthermore, model results suggest a relation between tail biting behaviour and the behavioural time budget of pigs. Recently published empirical studies also point in that direction (Larsen et al., 2016; Munsterhjelm et al., 2016).

## **7.2.2 In-depth modelling of feeding behaviour**

Similarly to tail biting behaviour, feeding behaviour in pigs has been studied intensively. It was shown to be affected by many internal (e.g. genotype and sex) and external factors (e.g. ambient temperature and group size) (De Haer & de Vries, 1993a; Nielsen et al., 1995; Quiniou et al., 2000). The internal causation of feeding behaviour, however, has been mechanistically modelled in several studies and is better understood than the internal causation of tail biting behaviour. The main emphasis in these studies is on predicting daily feed intake and growth of pigs under certain conditions. These models, however, do not include feeding patterns, such as meal frequency, meal size, meal duration, and between-meal intervals (e.g. De Lange, 1995; Wellock et al., 2004; Yoosuk et al., 2011), or use empirical (regression) equations to include feeding patterns, which means that they do not provide information about motivations underlying these patterns (e.g. Lewis & McGlone, 2008; Morgan et al., 2000). Therefore, a mechanistic and dynamic model was developed that included motivations underlying feeding behaviour and various feeding patterns (Chapter 3).

### **7.2.2.1 Integrating internal and external factors in feeding behaviour**

In Chapter 3, we first modelled the internal factors underlying feeding behaviour in pigs, such as growth capacity and gut load. Existing growth models (De Lange, 1995; NRC, 2012) were included in the model to affect energy use and requirement of a pig. This affected feeding motivation and feeding behaviour over time. Interaction between growth and motivation led to emergent feeding behaviour. The model shows that internal physiological factors, influenced by pig and diet characteristics, affect feeding motivation and consequently all feeding patterns. This model explains the change in feeding motivation and behaviour of pigs during the entire growing and fattening period from about 25 to 130 kg body weight. Although the model in Chapter 3 shows changing daily feeding patterns during growth of pigs, it is not able to reproduce observed feeding patterns of pigs within 24 hours. Pigs typically show an “alternans pattern” in feeding behaviour with two peaks during the day, of which the second peak exceeds the first one (e.g. Bornett et al., 2000a; De Haer & Merks, 1992). Including circadian rhythms of melatonin and cortisol as factors that drive

metabolism enabled to model this alternans pattern, creating a model that explains feeding motivation and feeding patterns of individually housed pigs within 24 hours (Chapter 4).

Our agent-based model as presented in Chapter 5 was built by extending the model described in Chapter 4, that reflected internal factors and feeding motivation of a pig, with social external factors, such as competition and social facilitation. This agent-based model allows testing the effect of interactions between internal and external factors on feeding behaviour and thus to study this behaviour and underlying motivation more in-depth. Model results show that daily feeding time affects competition and the number of conflicts for access to feed in group-housed pigs. Behavioural strategies (avoid or approach) for responding to these conflicts affect meal-based feeding patterns (e.g. meal frequency) and aggression in these pigs. Moreover, model results show that social facilitation is less important, although it can increase competition between pigs.

In Chapter 6, effects of various pig characteristics on individual variation in feeding, social interaction and growth patterns of group-housed pigs were explored. Model results show that pig characteristics, such as growth potential and dominance rank, can affect behaviour and growth patterns as well as abilities of pigs to cope with social constraints that inhibit them from feeding when they want to, for example, when other pigs use the feeder. Individual variation in dominance and coping style can reduce aggression at group level, but it can also make some pigs (e.g. low ranking pigs with a passive coping style) more susceptible to social constraints. Indications for social constraints can be deduced from a combination of feeding patterns, such as a decreased feed intake, lower feeding time and more and shorter meals.

Comprehensive and self-regulating models on feed intake control were found for feeding behaviour in sheep and cattle (e.g. Baumont et al., 2004; Gregorini et al., 2015; Sauvant et al., 1996), but were absent for pigs. Furthermore, the models used in sheep and cattle focused on the interaction of the animal with its physical environment, and not on social interactions. Development of dynamic and mechanistic models that increase understanding of physiological responses involved in pig growth and of impact of stressors (e.g. health and social) is still an important area for future research (Pettigrew, 2016). We, therefore, developed comprehensive and self-regulating models on feeding behaviour that increase understanding of underlying feeding motivation and physiological responses involved in pig growth (Chapter 3 and 4) and of impact of social constraints (Chapter 5 and 6).

### **7.3 The use of agent-based modelling for understanding animal welfare**

Agent-based modelling has shown to be useful for studying interactions between farm animal behaviour and the environment, especially in broiler chickens and pigs (e.g. Asher & Collins, 2012; Asher et al., 2013; Collins & Sumpter, 2007; Stricklin et al., 1995). Although these models included factors that explain behavioural patterns and may affect welfare (e.g. effect of social facilitation on excitatory and synchronized patterns of group feeding broiler chickens), they did not include welfare consequences. Furthermore, these models mainly considered the effect of physical effects of the environment, such as space and resource availability, on behaviour (Asher et al., 2009). No models were found that explore the relation between behaviour and welfare.

#### **7.3.1 Welfare assessment of tail biting behaviour**

The agent-based model of tail biting behaviour proved its use for increasing understanding of the behavioural patterns in tail biting (Chapter 2). Although the occurrence of tail biting behaviour in pigs by itself is an indicator for impaired welfare, it was difficult to assess the welfare of individual pigs in this model.

Impact of tail biting behaviour can be assessed with the various animal welfare approaches. These approaches include basic health and functioning, natural living and affective states (Fraser, 2008). Due to lack of quantitative data about tail biting characteristics (e.g. strength and duration of biting), we only modelled the first stage in tail biting behaviour, which is non-damaging tail biting. Non-damaging tail biting can develop into damaging tail biting behaviour, which is known to have a large impact on basic health and functioning of victims, for example, by injuries, inflammations, reduced growth and even death (Schrøder-Petersen & Simonsen, 2001; Taylor et al., 2010). Since we excluded damaging behaviour in the model, we were not able to assess the impact of tail biting behaviour on basic health and functioning of pigs involved in tail biting incidents. Furthermore, it can be expected that tail biting behaviour is an indicator for impaired natural living and affective states of pigs. An environment that does not provide opportunities to fulfil the motivation to explore can cause stress and frustration and can motivate pigs to start tail biting (D'Eath et al., 2014; Schrøder-Petersen & Simonsen, 2001). Tail biting behaviour might also affect natural behaviour and affective states of pigs that are not involved in tail biting incidents, because a higher level of arousal in these groups can increase the motivation to explore and thereby lead to more tail biting behaviour (Zonderland, 2010). More active and manipulative behaviour can be seen in groups with tail biting behaviour (Ursinus et al., 2014). How changes in behavioural patterns affect the natural living and affective states, however, is unknown. Tail biting behaviour, for example, might be a strategy to cope with a suboptimal environment and reduce or

even prevent welfare issues for the biter. It might also be that group mates that do not become a biter or victim have found a coping strategy to reduce overall stress (Munsterhjelm et al., 2013a).

Since the causation of tail biting behaviour and relations with most welfare issues are still poorly understood and quantitative data is lacking, it was not possible to develop a model that enabled welfare assessment based on tail biting behaviour. Including welfare consequences in the model would have required many assumptions that would have made the model results unreliable. The model shows the potential to analyse behavioural dynamics and welfare issues, provided that sufficient knowledge is available on the causation of the behaviour and relations with welfare.

### **7.3.2 Welfare assessment of feeding behaviour**

Compared to tail biting behaviour, the causation of feeding behaviour is relatively well understood, but its expression is less clearly associated with welfare issues. Feeding behaviour is essential for maintenance and growth of the body and thus for basic health and functioning of the animal. Pigs have their own expression of feeding behaviour (see Chapter 3), which is also part of a natural living and might impair welfare when this expression is restricted (Jensen & Toates, 1993). Furthermore, feeding behaviour is associated with affective states, in particular with hunger due to impaired feeding behaviour (D'Eath et al., 2009). Also a strong relation between feeding motivation and oral stereotypic behaviour, such as bar-biting and sham-shewing, has been demonstrated in feeding restricted sows (Lawrence & Terlouw, 1993).

In animal welfare assessment tools, welfare related to feeding behaviour is currently assessed indirectly, for example, by scoring the body condition of pigs and observing feed availability, such as the number of feeding spaces (Welfare Quality®, 2009). These measurements are relatively simple to conduct, but they do not directly measure feeding behaviour or the related welfare issue hunger. As reviewed by D'Eath et al. (2009), several measurements have been described as indicators for measuring hunger in animals, such as general activity, aggressive behaviour, feeding rate, heart rate and plasma glucocorticoids. These measurements, however, can be interpreted differently concerning animal welfare. Ambiguity in interpretation between studies may occur, for example, due to contrasting results on behavioural and physiological changes, and different assumptions about animal welfare approaches (D'Eath et al., 2009). Furthermore, these measurements do not necessarily reflect the actual level of hunger of an animal. Therefore, there is a need for better validated indicators to measure negative affective states related to hunger (D'Eath et al., 2009).

Affective states are not easily assessed. Researchers typically use two ways to find and validate measurements that reasonably correlate with the affective state of an animal: 1) by studying physiological and behavioural responses of animals when they are exposed to (un)pleasant stimuli or stressors, and 2) by comparing their physiological and behavioural changes with human responses (argument of analogy) (Kirkden & Pajor, 2006; Mason & Mendl, 1993).

Agent-based modelling can add to finding behaviours that serve as welfare indicators. Understanding the causation of behaviour as described in Chapter 3, 4, 5 and 6, contributes to understanding the effect of feeding motivation and nutritional, physical and social constraints on feeding and social interaction behaviour. Endocrine mechanisms that affect metabolism and feeding motivation stimulate feeding at specific times during the day (Chapter 4). Animals might especially be affected if they are restricted from feeding at these times, for example, by feeding regimes or social factors, such as competition. Results in Chapter 5 show, for example, that feeder occupation above 35% per hour during the night and above 80% per hour during the day can indicate high social constraints and increased aggression. These results also show how competition among more aggressive pigs can increase displacements at the feeder and can increase meal frequency, whereas competition among less aggressive pigs can decrease displacements and meal frequency. This suggests that a high feeder occupation and a change in meal patterns (i.e. meal frequency, meal size and duration) can indicate social constraints and can be potential indicators for animal welfare issues in pigs.

In Chapter 6, however, results also show that indicators for animal welfare assessment at group level, are not necessarily be suitable for assessing animal welfare at individual level. Although increased meal frequency indicated increased conflicts and aggression in groups (Chapter 5), an increased meal frequency was not necessarily an indication of conflicts and aggression at individual level. Variation in meal patterns among pigs can also be a result of a physiological factor, such as a positive feedback signal associated with stomach load that reinforces feeding behaviour and stimulates longer meals. Therefore, pigs with an increased meal frequency could also be high ranking pigs with physiologically driven smaller meals, which experience few constraints. Furthermore, pigs that experience most constraints might even have a lower meal frequency when they cannot gain access to the feeder. Another example of a feeding behaviour with varying value as welfare indicator is feeding rate. Feeding rate has been suggested to reflect the social constraints at group level (Nielsen, 1999). Results in Chapter 5 indeed confirm that feeding rate can be an indicator of social constraints at group level. At individual level, however, feeding rate might not be a suitable indicator for social constraints, because both pig characteristics that affect physiological factors (e.g. protein deposition) and pig characteristics that affect behavioural strategies (e.g. coping style) can affect feeding



rate (Chapter 6). Furthermore, slow and fast feeder pigs did not differ in dominance rank, while low ranking pigs are most expected to be socially constrained. Low ranking pigs, however, differed in various feeding patterns, such as a lower feed intake, a lower feeding time and many small and brief meals. Therefore, a combination of these patterns might be suitable for identifying socially constrained pigs. For instance, a decreased level of feed intake in combination with a change in meal frequency and decreased morning peak can indicate social constraints to reaching the feeder. Although the use of feeding patterns as welfare indicator at individual and group level still needs to be validated with empirical data, combining agent-based modelling with empirical data allows to find behaviours that can serve as welfare indicators. This method, therefore, seems to be a useful novel approach in the search for animal-based welfare indicators.

Changes in feeding behaviour have been associated with multiple welfare issues, such as health problems (Nielsen et al., 2016) and tail biting behaviour (Wallenbeck & Keeling, 2013). For future studies, it would be interesting to evaluate feeding behaviour as an indicator to detect or prevent health problems and to evaluate its relation to tail biting behaviour. In this respect, exploration behaviour is potentially also interesting to model and evaluate as a welfare indicator. Like feeding behaviour, exploration behaviour has been studied intensively (e.g. Averós et al., 2010; Day et al., 1996; Stolba & Wood-Gush, 1980; Studnitz et al., 2007) and has been associated with animal welfare issues, such as impaired expression of natural behaviours and of abnormal behaviours, such as tail biting (Moinard et al., 2003; Temple et al., 2011). The relation with welfare, however, is not always clear. Measurements of exploration behaviour can be situation dependent and difficult to interpret (Temple et al., 2011). Understanding the underlying motivation of exploration behaviour, therefore, can contribute to assessing exploration behaviour as a welfare indicator. Furthermore, understanding motivational systems underlying feeding and exploration behaviour might be an important step in truly understanding tail biting behaviour and its welfare consequences.

Understanding how behaviours can be interpreted as welfare indicators can be especially valuable since novel techniques, such as automatic feeders and individual recognition (e.g. by radio frequency identification), allow to more easily measure various feeding and other behavioural patterns in pigs and to detect changes in these patterns (Maselyne et al., 2015). Automatic and continuous measurements of all kind of animal characteristics and features can be used to monitor their welfare (Berckmans, 2014; Matthews et al., 2016; Nielsen et al., 2016; Rushen et al., 2012). Suitability of feeding behaviour measurements for application as health or welfare indicator, however, should be further validated (Maselyne et al., 2015).

## 7.4 Application of an integrated model for sustainability analysis

The model presented in Chapter 6 allows to analyse feeding, social interaction and growth patterns of pigs at individual and group level. It includes measurements that can indicate welfare issues, such as number of conflicts, received displacements, number of interactions won or lost, and level of feeding motivation (hunger). It also includes measurements that can indicate productivity, such as body weight gain (in protein and fat deposition) and feed conversion ratio. The model, therefore, can be used to analyse trade-offs and synergies between behaviours and growth performance under different conditions, such as various group sizes, and homogeneity versus heterogeneity of groups (e.g. in growth potential, body weight and coping style).

To illustrate the potential of the model to analyse trade-offs and synergies, we explored the effect of differences in coping style among group-housed pigs on animal welfare and productivity performance. We simulated three experimental conditions: groups with only passive copers (pigs with a high threshold to compete for food of 0.5), groups with only active copers (pigs with a low threshold to compete for food of 0.1), and mixed groups with passive and active copers (pigs with varying values for the threshold to compete, based on a normal distribution). This experimental setup is comparable to the empirical study of Hessing et al. (1994).

**Table 1.** Mean  $\pm$  Standard Deviation of productivity and animal welfare measurements in groups composed of pigs with passive and/or pigs with active coping styles.\*

	Passive coping style	Passive/active coping style	Active coping style
<i>Productivity indicators</i>			
Feed intake (g/day)	2280 $\pm$ 24	2262 $\pm$ 21	2256 $\pm$ 16
Final body weight (kg)	103.5 $\pm$ 1.6	103.2 $\pm$ 1.3	103.1 $\pm$ 1.3
% protein	13.8 $\pm$ 0.3	13.9 $\pm$ 0.2	13.9 $\pm$ 0.2
% lipid	28.9 $\pm$ 0.2	28.8 $\pm$ 0.3	28.7 $\pm$ 0.2
Body weight gain (g/day)	965 $\pm$ 20	962 $\pm$ 17	961 $\pm$ 13
Potential PD (g/day)	144 $\pm$ 5	145 $\pm$ 5	145 $\pm$ 4
Growth gap PD (g/day)	13.6 $\pm$ 1.6	13.5 $\pm$ 1.6	13.5 $\pm$ 1.4
Feed conversion ratio (g/g)	2.35 $\pm$ 0.03	2.34 $\pm$ 0.03	2.34 $\pm$ 0.02
<i>Animal welfare indicators</i>			
Conflicts (no.)	55.9 $\pm$ 1.1	51.3 $\pm$ 1.7	48.5 $\pm$ 1.8
Aggressive interactions (no.)	2.8 $\pm$ 1.0	11.3 $\pm$ 4.3	24.4 $\pm$ 8.4
Duration feeding motivation (min/day)	4.9 $\pm$ 0.1	4.6 $\pm$ 0.1	4.3 $\pm$ 0.0
Average feeding motivation level	0.47 $\pm$ 0.00	0.44 $\pm$ 0.01	0.42 $\pm$ 0.00
Highest motivation level	2.15 $\pm$ 0.02	2.05 $\pm$ 0.02	1.99 $\pm$ 0.02

\* Mean values of groups with 10 pigs over 80 simulation days. Simulations were repeated 14 times.

Model results show some variation in productivity and animal welfare indicators between experimental groups (Table 1). Feed intake was highest in groups with passive copers and lowest in groups with active copers, but further productivity indicators were rather similar between groups. Groups with only passive copers showed fewer food-related aggressive interactions, but more conflicts (meaning that a pig wanted to feed when the feeder was already used by another pig), and a higher level and longer duration of feeding motivation compared to other groups. Groups with only active copers showed opposite results, whereas groups with both passive and active copers were in between results of the two other groups.

Our model results only partly correspond to results of Hessing et al. (1994). In that study, groups with mixed coping style had a higher daily body weight gain (801 g/day) than groups with only passive (773 g/day) or active copers (761 g/day). This is in contrast with our results, in which body weight gain was rather similar between groups. This difference might be due to health conditions of pigs. Post mortem diagnosis in the study of Hessing et al. (1994) showed that a high percentage of pigs in the empirical study suffered from pleurisy, haemorrhages on the heart muscle, stomach wall damage and stenose. Prevalence of haemorrhages on the heart muscle was similar for pigs in all groups, but prevalence of pleurisy tended to be lowest in pigs of mixed coping style groups, and prevalence of severe stomach wall damage was highest in pigs of passive coping style groups. The health conditions in Hessing et al. (1994) were associated with decreased body weight gain, i.e. 18 g/day with pleurisy, 35 g/day with severe stomach wall damage and 65 g/day with stenose (which was included in the most severe score for stomach wall damage). The lower body weight gain in the empirical groups with only passive or active copers, therefore, was related to health problems.

We, however, modelled healthy animals and did not include a relation between social stress and disease susceptibility. Higher prevalence of health problems in groups with only passive or active copers, however, might be related to increased disease susceptibility due to social stress (Hessing et al., 1994). The higher prevalence of severe stomach wall damage found in the empirical groups with only passive copers might be related to social stress caused by conflicts and feeding motivation levels, which were higher in the simulated groups with only passive copers. The higher prevalence of pleurisy in groups of only active copers might be related to food-related aggressive behaviour, which was higher in the simulated groups with only active copers.

Our results suggest that differences in coping style among group-housed pigs do not affect productivity directly, but can affect animal welfare due to food-related aggressive behaviour, conflicts and feeding motivation levels that can cause social stress. These model results are provided as an illustration to show how we can use the

model to analyse trade-offs and synergies between welfare and productivity performance in pigs under various conditions. To draw further conclusions, the model results should be analysed and validated in more detail, such as the relation between social stress, disease susceptibility and growth of pigs.

## 7.5 Methodological challenges in this thesis

In this thesis, we demonstrated that agent-based modelling is useful for understanding behaviour and welfare issues. The method also has challenges because agent-based models are harder to develop, analyse and communicate than traditional systemic models (Grimm et al., 1999). This applies in particular to the agent-based model of feeding behaviour described in this thesis. This model required relatively comprehensive mechanisms to reflect the motivational system underlying feeding behaviour and the interactions with internal and external factors. A disadvantage of such a model is that it needs many parameters and relationships among them, which increases the risk of errors and, if relationships are not well understood, can make a model unreliable (Asher et al., 2009). To deal with this issue, pattern-oriented modelling was used (see Chapter 2). Pattern-oriented modelling is a method in which multiple patterns at different hierarchical levels are identified and used to systematically develop and analyse a model (Grimm & Railsback, 2012; Grimm et al., 2005). In this thesis, the levels were motivation, behaviour and welfare (sustainability). Pattern-oriented modelling allowed to determine the necessary structure and variables, to select and test submodels that represent processes on a certain level, and to find adequate parameter values with calibration (Grimm & Railsback, 2012; Grimm et al., 2005). The feeding model, for example, consisted of three submodels: *Motivation*, *Behavioural decision-making* and *Growth*. The model was built stepwise, in which submodels were also analysed and calibrated separately: first, the submodels *Growth* and *Behavioural decision-making* (Chapter 3); second, variables that represented hormonal affects in the submodel *Motivation* (Chapter 4); and third, variables that represented social effects in the submodels *Motivation* and *Behavioural decision-making*. Stepwise modelling allowed to properly understand and analyse the model before more mechanisms were included, and thus decreased the risk of errors.

A major challenge in agent-based modelling is model analysis. This means understanding and explaining model behaviour. Since an agent-based model can contain many input parameters and many mechanisms, and can generate nonlinear emergent outputs, model analysis is not straightforward. To begin with, one of the challenges is that model analysis includes large amounts of output data. This can impede interpretation and identification of relevant results (Lee et al., 2015). For understanding agent-based models and their output, model experiments should be performed based on hypotheses, and several (statistical) strategies can be used to understand model output, such as descriptive statistics, contrasting scenarios,

quantifying correlative relationships and comparing model output to empirical patterns (Railsback & Grimm, 2012). In Chapter 4 and 5, for example, contrasting scenarios were tested to quantify effects of hormonal circadian rhythms and behavioural strategies on feeding patterns. Furthermore, model analysis should include examination of relations between parameter settings and model results, such as a sensitivity analysis (Lee et al., 2015; Ten Broeke et al., 2016). A sensitivity analysis can show the relative importance of certain parameters and processes in the model, and evaluate the robustness and uncertainty of emergent results (Ten Broeke et al., 2016). In agent-based models, sensitivity analysis is challenging due to various non-linear effects (e.g. in interaction between parameters and normality of output) (Lee et al., 2015). A commonly used method is a local sensitivity analysis, in which one factor at a time is changed while other parameters are kept constant. Although this method might overlook important parameter interactions, it may yield the best results for gaining insight into mechanisms and patterns in the model (Ten Broeke et al., 2016). In this thesis, all models were examined using a local sensitivity analysis, in which one parameter at a time was changed.

Another challenge, and essential part in modelling, is validation of the model. Models can be based on scientific literature and experts, and should preferably also be tested or validated on independent datasets (Bryson et al., 2007). Where possible, model parameters were parameterised with empirical data in this thesis. For example, the energy and threshold variables for causation of other behaviours than feeding behaviour were calibrated to obtain time budgets of pigs as observed in commercially and barren housed growing pigs. Such a parameterisation can reduce applicability of the model to other than assumed conditions, and can increase error risks in model results if the empirical dataset was not representative for empirical results, however, it can also increase objectivity of the model (Collins & Part, 2013). Lack of available quantitative data can be a constraint for modelling. Validation on independent empirical data is impossible when available data is used for constructing the model and no additional data is available (Collins & Part, 2013). An advantage for agent-based models of farm animals compared to ecological animal models or social models in humans is the availability of extensive data of measurements on animals and highly standardized environments (e.g. group size and diet characteristics). In this thesis, we validated model results at multiple levels (e.g. at behavioural level, motivational level and physiological level in Chapter 4) and, where possible, against independent empirical data. An advantage of the stepwise modelling approach in this thesis was that aspects of the model that included parameterisation and assumption could be tested and validated in steps as well. Some lacking data could be collected by testing various scenarios in the model. For example, the effect of avoidance and approach on feeding patterns (Chapter 5).

Due to complexity of agent-based models, both describing and communicating them can be difficult (Grimm et al., 1999). To standardize model descriptions in this thesis, the ODD (Overview, Design concepts, and Details) protocol was used (Grimm et al., 2006; Grimm et al., 2010). Such protocols improve clarity, replicability, and confidence in agent-based modelling results (Lee et al., 2015).

## 7.6 Conclusions

Using an agent-based approach, we showed that redirected motivation of explorative behaviour can cause tail biting behaviour, and that the incidence of tail biting between groups can vary by chance. Preference to bite a lying pig and an effect of biting on the behavioural motivations of a victim were of minor importance to this incidence. The behavioural time budget of a pig, however, might be important in predisposing pigs or preventing them from becoming involved in biting incidents.

By modelling growth in combination with motivational decisions, variation in growth and feeding patterns over the entire growth period of a growing fattening pig can be explained. Moreover, this model enables understanding of the importance of physiological factors, and pig and diet characteristics underlying feeding motivation.

Including circadian rhythms of melatonin and cortisol in the motivational feeding model enabled to simulate a typical “alternans pattern” in feeding behaviour (i.e. two peaks during the day, of which the second peak exceeds the first one). Model results indicate that the hormones melatonin and cortisol directly drive energy metabolism affecting feeding behaviour, whereas other hormones, such as leptin and ghrelin, regulate feeding behaviour depending on the energy status of the animal.

Integrating internal and external factors in an agent-based model on feeding behaviour enabled in-depth study of feeding motivation and behaviour. We showed that internal physiological factors, influenced by pig and diet characteristics, affected feeding rate, meal duration, meal size, meal frequency, total feed intake and feeding time during a day. These feeding patterns, and especially feeding time, can affect competition and cause conflicts for feed in group-housed pigs. Social facilitation only slightly increased competition between pigs. Changed feeding patterns, such as meal frequency, feeding rate, and feeder occupation during day and night, are promising indicators for animal welfare at group level in pig production systems.

Variation in feeding, social interaction and growth patterns among pigs can be explained by variation in pig characteristics that, on the one hand, affect physiological factors and, on the other hand, affect behavioural strategies to approach or avoid conflicts at the feeder. Individual variation in behavioural strategies can reduce aggression at group level, but can make individual pigs more susceptible to social constraints. Feeding patterns, such as feed intake, feeding rate and meal frequency,

can say something different about animal welfare at group versus individual level. We suggest that a combination of these feeding patterns may be suitable for identifying pigs with welfare risks within a group.

Agent-based modelling appeared a useful method to understand animal behaviour and underlying motivations. It contributed to further understanding of tail biting and feeding behaviour in pigs in all its complexity. Furthermore, agent-based modelling showed to be a novel method to find and assess behaviours as welfare indicators, and to contribute to understanding trade-offs and synergies between sustainability issues, such as animal welfare and productivity.





# References

- Andersen, I.L., Nævdal, E., Bakken, M., & Bøe, K.E. (2004). Aggression and group size in domesticated pigs, *Sus scrofa*: 'when the winner takes it all and the loser is standing small'. *Animal Behaviour*, 68(4), 965-975.
- Andersen, I.L., Nævdal, E., Bøe, K.E., & Bakken, M. (2006). The significance of theories in behavioural ecology for solving problems in applied ethology—Possibilities and limitations. *Applied Animal Behaviour Science*, 97(1), 85-104.
- Andersson, H., Lillpers, K., Rydhmer, L., & Forsberg, M. (2000). Influence of light environment and photoperiod on plasma melatonin and cortisol profiles in young domestic boars, comparing two commercial melatonin assays. *Domestic Animal Endocrinology*, 19(4), 261-274.
- Arnott, G., & Elwood, R.W. (2008). Information gathering and decision making about resource value in animal contests. *Animal Behaviour*, 76(3), 529-542.
- Arruda, A.G., Friendship, R., Carpenter, J., Greer, A., & Poljak, Z. (2016). Evaluation of control strategies for porcine reproductive and respiratory syndrome (PRRS) in swine breeding herds using a discrete event agent-based model. *PLoS ONE*, 11(11), e0166596.
- Aschoff, J. (1957). Aktivitätsmuster der tagesperiodik. *Naturwissenschaften*, 44(13), 361-367.
- Aschoff, J. (1963). Comparative physiology: diurnal rhythms. *Annual Review of Physiology*, 25(1), 581-600.
- Aschoff, J. (1966). Circadian Activity Pattern with Two Peaks. *Ecology*, 47(4), 657-662.
- Asher, L., & Collins, L.M. (2012). Assessing synchrony in groups: Are you measuring what you think you are measuring? *Applied Animal Behaviour Science*, 138(3-4), 162-169.
- Asher, L., Collins, L.M., Ortiz-Pelaez, A., Drewe, J.A., Nicol, C.J., & Pfeiffer, D.U. (2009). Recent advances in the analysis of behavioural organization and interpretation as indicators of animal welfare. *Journal of the Royal Society Interface*, 6(41), 1103-1119.
- Asher, L., Collins, L.M., Pfeiffer, D.U., & Nicol, C.J. (2013). Flocking for food or flockmates? *Applied Animal Behaviour Science*, 147(1-2), 94-103.
- Atkinson, H.C., & Waddell, B.J. (1997). Circadian variation in basal plasma corticosterone and adrenocorticotropin in the rat: sexual dimorphism and changes across the estrous cycle. *Endocrinology*, 138(9), 3842-3848.
- Averós, X., Brossard, L., Dourmad, J.-Y., de Greef, K.H., Edge, H.L., Edwards, S.A., & Meunier-Salaün, M.-C. (2010). A meta-analysis of the combined effect of housing and environmental enrichment characteristics on the behaviour and performance of pigs. *Applied Animal Behaviour Science*, 127(3-4), 73-85.
- Babin-Fenske, J., & Anand, M. (2011). Agent-based simulation of effects of stress on forest tent caterpillar (*Malacosoma disstria* Hübner) population dynamics. *Ecological Modelling*, 222(14), 2561-2569.
- Bae, Y.J., & Kratzsch, J. (2015). Corticosteroid-binding globulin: Modulating mechanisms of bioavailability of cortisol and its clinical implications. *Best Practice & Research: Clinical Endocrinology & Metabolism*, 29(5), 761-772.

- Barnett, J., Winfield, C., Cronin, G., & Makin, A. (1981). Effects of photoperiod and feeding on plasma corticosteroid concentrations and maximum corticosteroid-binding capacity in pigs. *Australian Journal of Biological Sciences*, 34(6), 577-586.
- Basset-Mens, C., & van der Werf, H.M.G. (2005). Scenario-based environmental assessment of farming systems: the case of pig production in France. *Agriculture, Ecosystems & Environment*, 105(1-2), 127-144.
- Bastianelli, D., Sauvant, D., & Rérat, A. (1996). Mathematical modeling of digestion and nutrient absorption in pigs. *Journal of Animal Science*, 74(8), 1873-1887.
- Batterham, E.S., & Bayley, H.S. (1989). Effect of frequency of feeding of diets containing free or protein-bound lysine on the oxidation of [C]lysine or [C]phenylalanine by growing pigs. *British Journal of Nutrition*, 62(03), 647-655.
- Baumont, R., Cohen-Salmon, D., Prache, S., & Sauvant, D. (2004). A mechanistic model of intake and grazing behaviour in sheep integrating sward architecture and animal decisions. *Animal Feed Science and Technology*, 112(1-4), 5-28.
- Beattie, V.E., Breuer, K., O'Connell, N.E., Sneddon, I.A., Mercer, J.T., Rance, K.A., Sutcliffe, M.E.M., & Edwards, S.A. (2005). Factors identifying pigs predisposed to tail biting. *Animal Science*, 80(03), 307-312.
- Beattie, V.E., O'Connell, N.E., & Moss, B.W. (2000). Influence of environmental enrichment on the behaviour, performance and meat quality of domestic pigs. *Livestock Production Science*, 65(1-2), 71-79.
- Berckmans, D. (2014). Precision livestock farming technologies for welfare management in intensive livestock systems. *Scientific and Technical Review of the Office International des Epizooties*, 33(1), 189-196.
- Berthoud, H.-R., & Morrison, C. (2008). The brain, appetite, and obesity. *Annual Review of Psychology*, 59(1), 55-92.
- Bigelow, J.A., & Hout, T.R. (1988). Feeding and drinking patterns in young pigs. *Physiology & Behavior*, 43(1), 99-109.
- Black, J., Williams, B., & Gidley, M. (2009). Metabolic regulation of feed intake in monogastric mammals. In D. Torrallardona & E. Roura (Eds.), *Voluntary Feed Intake in Pigs* (pp. 189-213). Wageningen, the Netherlands: Wageningen Academic Publishers.
- Black, J.L. (1995). Modelling energy metabolism in the pig - critical evaluation of a simple reference model. In P. J. Moughan, M. W. A. Verstegen, & M. I. Visser-Reyneveld (Eds.), *Modelling growth in the pig* (pp. 87-102). Wageningen, the Netherlands: Wageningen Pers.
- Black, J.L., & de Lange, C.F.M. (1995). Introduction to the principles of nutrient partitioning for growth. In P. J. Moughan, M. W. A. Verstegen, & M. I. Visser-Reyneveld (Eds.), *Modelling growth in the pig* (pp. 33-45). Wageningen, the Netherlands: Wageningen Pers.
- Blanes-Vidal, V., Hansen, M.N., Pedersen, S., & Rom, H.B. (2008). Emissions of ammonia, methane and nitrous oxide from pig houses and slurry: Effects of rooting material, animal activity and ventilation flow. *Agriculture, Ecosystems & Environment*, 124(3-4), 237-244.
- Blokhuis, H.J., Keeling, L.J., Gavinelli, A., & Serratos, J. (2008). Animal welfare's impact on the food chain. *Trends in Food Science & Technology*, 19, Supplement 1, S79-S87.

- Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., & Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior*, 92(3), 375-397.
- Bolhuis, J.E., Schouten, W.G.P., Schrama, J.W., & Wiegant, V.M. (2005a). Behavioural development of pigs with different coping characteristics in barren and substrate-enriched housing conditions. *Applied Animal Behaviour Science*, 93(3-4), 213-228.
- Bolhuis, J.E., Schouten, W.G.P., Schrama, J.W., & Wiegant, V.M. (2005b). Individual coping characteristics, aggressiveness and fighting strategies in pigs. *Animal Behaviour*, 69(5), 1085-1091.
- Bornett, H.L.I., Morgan, C.A., Lawrence, A.B., & Mann, J. (2000a). The effect of group housing on feeding patterns and social behaviour of previously individually housed growing pigs. *Applied Animal Behaviour Science*, 70(2), 127-141.
- Bornett, H.L.I., Morgan, C.A., Lawrence, A.B., & Mann, J. (2000b). The flexibility of feeding patterns in individually housed pigs. *Animal Science*, 70(3), 457-469.
- Borrisser-Pairó, F., Kallas, Z., Panella-Riera, N., Avena, M., Ibáñez, M., Olivares, A., Gil, J.M., & Oliver, M.A. (2016). Towards entire male pigs in Europe: A perspective from the Spanish supply chain. *Research in Veterinary Science*, 107, 20-29.
- Botermans, J.A.M., Georgsson, L., Weström, B.R., Olsson, A.-C., & Svendsen, J. (2000). Effect of Feeding Environment on Performance, Injuries, Plasma Cortisol and Behaviour in Growing-finishing Pigs: Studies on Individual Pigs Housed in Groups. *Acta Agriculturae Scandinavica, Section A — Animal Science*, 50(4), 250-262.
- Boumans, I.J.M.M., Bokkers, E.A.M., Hofstede, G.J., & de Boer, I.J.M. (2015). Understanding feeding patterns in growing pigs by modelling growth and motivation. *Applied Animal Behaviour Science*, 171, 69-80.
- Boumans, I.J.M.M., de Boer, I.J.M., Hofstede, G.J., & Bokkers, E.A.M. (2017a). How social factors and behavioural strategies affect feeding and social interaction patterns in pigs in an agent-based model. (*submitted*).
- Boumans, I.J.M.M., de Boer, I.J.M., Hofstede, G.J., la Fleur, S.E., & Bokkers, E.A.M. (2017b). The importance of hormonal circadian rhythms in daily feeding patterns: An illustration with simulated pigs. *Hormones and Behavior*, 93, 82-93.
- Boumans, I.J.M.M., Hofstede, G.J., Bolhuis, J.E., de Boer, I.J.M., & Bokkers, E.A.M. (2016). Agent-based modelling in applied ethology: An exploratory case study of behavioural dynamics in tail biting in pigs. *Applied Animal Behaviour Science*, 183, 10-18.
- Bracke, M.B.M. (2009). Rope test may indicate efficacy of tail-biting treatments in growing pigs. *Animal Welfare*, 18(3), 263-266.
- Bracke, M.B.M., Hulsegge, B., Keeling, L., & Blokhuis, H.J. (2004a). Decision support system with semantic model to assess the risk of tail biting in pigs: 1. Modelling. *Applied Animal Behaviour Science*, 87(1-2), 31-44.
- Bracke, M.B.M., Hulsegge, B., Keeling, L., & Blokhuis, H.J. (2004b). Decision support system with semantic model to assess the risk of tail biting in pigs: 2. 'Validation'. *Applied Animal Behaviour Science*, 87(1-2), 45-54.

- Brouns, F., & Edwards, S.A. (1994). Social rank and feeding behaviour of group-housed sows fed competitively or ad libitum. *Applied Animal Behaviour Science*, 39(3–4), 225-235.
- Brouns, F., Edwards, S.A., & English, P.R. (1994). Effect of dietary fibre and feeding system on activity and oral behaviour of group housed gilts. *Applied Animal Behaviour Science*, 39(3–4), 215-223.
- Brouns, F., Edwards, S.A., & English, P.R. (1997). The effect of dietary inclusion of sugar-beet pulp on the feeding behaviour of dry sows. *Animal Science*, 65(01), 129-133.
- Brunberg, E., Wallenbeck, A., & Keeling, L.J. (2011). Tail biting in fattening pigs: Associations between frequency of tail biting and other abnormal behaviours. *Applied Animal Behaviour Science*, 133(1-2), 18-25.
- Bryson, J.J., Ando, Y., & Lehmann, H. (2007). Agent-based modelling as scientific method: a case study analysing primate social behaviour. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362(1485), 1685-1698.
- Bubenik, G.A., Pang, S.F., Cockshut, J.R., Smith, P.S., Grovum, L.W., Friendship, R.M., & Hacker, R.R. (2000). Circadian variation of portal, arterial and venous blood levels of melatonin in pigs and its relationship to food intake and sleep. *Journal of Pineal Research*, 28(1), 9-15.
- Camerlink, I., Arnott, G., Farish, M., & Turner, S.P. (2016). Complex contests and the influence of aggressiveness in pigs. *Animal Behaviour*, 121, 71-78.
- Camerlink, I., Turner, S.P., Farish, M., & Arnott, G. (2015). Aggressiveness as a component of fighting ability in pigs using a game-theoretical framework. *Animal Behaviour*, 108, 183-191.
- CBS. (2016, 23-9-2016). Varkensbedrijven: steeds meer varkens per bedrijf. Retrieved 21-03-2017, 2017, from <https://www.cbs.nl/nl-nl/achtergrond/2016/33/varkensbedrijven-steeds-meer-varkens-per-bedrijf>
- Chemineau, P. (2016). Invited review: Importance of animal health and welfare for the stability of the three pillars of sustainability of livestock systems. *Advances in Animal Biosciences*, 7(2), 208-214.
- Claustrat, B., Brun, J., & Chazot, G. (2005). The basic physiology and pathophysiology of melatonin. *Sleep Medicine Reviews*, 9(1), 11-24.
- Clayton, D.A. (1978). Socially facilitated behavior. *The Quarterly Review of Biology*, 53(4), 373-392.
- Collins, L., & Part, C. (2013). Modelling farm animal welfare. *Animals*, 3(2), 416-441.
- Collins, L.M., Asher, L., Pfeiffer, D.U., Browne, W.J., & Nicol, C.J. (2011). Clustering and synchrony in laying hens: The effect of environmental resources on social dynamics. *Applied Animal Behaviour Science*, 129(1), 43-53.
- Collins, L.M., & Sumpter, D.J.T. (2007). The feeding dynamics of broiler chickens. *Journal of the Royal Society Interface*, 4(12), 65-72.
- Corbalán-Tutau, D., Madrid, J.A., Nicolás, F., & Garaulet, M. (2014). Daily profile in two circadian markers “melatonin and cortisol” and associations with metabolic syndrome components. *Physiology & Behavior*, 123, 231-235.
- Cornetto, T., Estevez, I., & Douglass, L.W. (2002). Using artificial cover to reduce aggression and disturbances in domestic fowl. *Applied Animal Behaviour Science*, 75(4), 325-336.
- Cummings, D.E., & Overduin, J. (2007). Gastrointestinal regulation of food intake. *Journal of Clinical Investigation*, 117(1), 13-23.

- D'Eath, R.B., Tolkamp, B.J., Kyriazakis, I., & Lawrence, A.B. (2009). 'Freedom from hunger' and preventing obesity: the animal welfare implications of reducing food quantity or quality. *Animal Behaviour*, 77(2), 275-288.
- D'Eath, R.B., Arnott, G., Turner, S.P., Jensen, T., Lahrmann, H.P., Busch, M.E., Niemi, J.K., Lawrence, A.B., & Sandøe, P. (2014). Injurious tail biting in pigs: how can it be controlled in existing systems without tail docking? *Animal*, 8(09), 1479-1497.
- Dallman, M.F., la Fleur, S.E., Pecoraro, N.C., Gomez, F., Houshyar, H., & Akana, S.F. (2004). Minireview: Glucocorticoids—food intake, abdominal obesity, and wealthy nations in 2004. *Endocrinology*, 145(6), 2633-2638.
- Dawkins, M.S. (2017). Animal welfare and efficient farming: is conflict inevitable? *Animal Production Science*, 57(2), 201-208.
- Day, J.E.L., Kyriazakis, I., & Lawrence, A.B. (1995). The effect of food deprivation on the expression of foraging and exploratory behaviour in the growing pig. *Applied Animal Behaviour Science*, 42(3), 193-206.
- Day, J.E.L., Kyriazakis, I., & Lawrence, A.B. (1996). An investigation into the causation of chewing behaviour in growing pigs: The role of exploration and feeding motivation. *Applied Animal Behaviour Science*, 48(1-2), 47-59.
- Day, J.E.L., Kyriazakis, I., & Rogers, P.J. (1998). Food choice and intake: towards a unifying framework of learning and feeding motivation. *Nutrition Research Reviews*, 11(1), 25-44.
- De Boer, I.J.M. (2012). Innovation born of Integration. Moving towards sustainable production of animal-source food *Inaugural lecture upon taking up the post of Professor of Animal Production Systems*. Wageningen, the Netherlands: Wageningen University.
- De Guia, R.M., Rose, A.J., & Herzig, S. (2014). Glucocorticoid hormones and energy homeostasis. *Hormone Molecular Biology and Clinical Investigation*, 19(2), 117-128.
- De Haer, L.C.M., & de Vries, A.G. (1993a). Effects of genotype and sex on the feed intake pattern of group housed growing pigs. *Livestock Production Science*, 36(3), 223-232.
- De Haer, L.C.M., & de Vries, A.G. (1993b). Feed intake patterns of and feed digestibility in growing pigs housed individually or in groups. *Livestock Production Science*, 33(3-4), 277-292.
- De Haer, L.C.M., Luiting, P., & Aarts, H.L.M. (1993). Relations among individual (residual) feed intake, growth performance and feed intake pattern of growing pigs in group housing. *Livestock Production Science*, 36(3), 233-253.
- De Haer, L.C.M., & Merks, J.W.M. (1992). Patterns of daily food intake in growing pigs. *Animal Science*, 54(01), 95-104.
- De Lange, C.F.M. (1995). Framework for a simplified model to demonstrate principles of nutrient partitioning for growth in the pig. In P. J. Moughan, M. W. A. Verstegen, & M. I. Visser-Reyneveld (Eds.), *Modelling growth in the pig* (pp. 71-85). Wageningen, the Netherlands: Wageningen Pers.
- De Lange, C.F.M., Morel, P.C.H., & Birkett, S.H. (2003). Modeling chemical and physical body composition of the growing pig. *Journal of Animal Science*, 81(14 suppl 2), E159-E165.

- Dekker, S.E.M., de Boer, I.J.M., Vermeij, I., Aarnink, A.J.A., & Groot Koerkamp, P.W.G. (2011). Ecological and economic evaluation of Dutch egg production systems. *Livestock Science*, 139(1-2), 109-121.
- Demaria-Pesce, V.H., & Nicolaïdis, S. (1998). Mathematical determination of feeding patterns and its consequence on correlational studies. *Physiology & Behavior*, 65(1), 157-170.
- Den Ouden, M., Nijsing, J.T., Dijkhuizen, A.A., & Huirne, R.B.M. (1997). Economic optimization of pork production-marketing chains: I. Model input on animal welfare and costs. *Livestock Production Science*, 48(1), 23-37.
- Dolman, M.A., Vrolijk, H.C.J., & de Boer, I.J.M. (2012). Exploring variation in economic, environmental and societal performance among Dutch fattening pig farms. *Livestock Science*, 149(1-2), 143-154.
- Dourmad, J.-Y., Ryschawy, J., Trousson, T., Bonneau, M., González, J., Houwers, H., Hviid, M., Zimmer, C., Nguyen, T., & Morgensen, L. (2014). Evaluating environmental impacts of contrasting pig farming systems with life cycle assessment. *Animal*, 8(12), 2027-2037.
- Duncan, I. (2005). Science-based assessment of animal welfare: farm animals. *Revue scientifique et technique-Office international des epizooties*, 24(2), 483.
- Duncan, I.J. (1998). Behavior and behavioral needs. *Poultry Science*, 77(12), 1766-1772.
- Eckel-Mahan, K., & Sassone-Corsi, P. (2013). Metabolism and the circadian clock converge. *Physiological Reviews*, 93(1), 107-135.
- EFSA. (2007a). Scientific opinion of the panel on animal health and welfare on a request from the commission on animal health and welfare in fattening pigs in relation to housing and husbandry *The EFSA Journal* (Vol. 564, pp. 1-14).
- EFSA. (2007b). Scientific opinion of the panel on animal health and welfare on a request from the Commission on risks associated with tail biting in pigs and possible means to reduce the need for tail docking considering the different housing and husbandry systems *The EFSA journal* (Vol. 611, pp. 1-13): European Food Safety Authority.
- Eckel, E.D., Savenije, B., Schouten, W.G.P., Wiegant, V.M., & Tielen, M.J.M. (1997). The effects of mixing on behavior and circadian parameters of salivary cortisol in pigs. *Physiology & Behavior*, 62(1), 181-184.
- Estevez, I., Andersen, I.-L., & Nævdal, E. (2007). Group size, density and social dynamics in farm animals. *Applied Animal Behaviour Science*, 103(3-4), 185-204.
- Evers, E., de Vries, H., Spruijt, B.M., & Sterck, E.H.M. (2014). The EMO-model: an agent-based model of orimate social behavior regulated by two emotional dimensions, anxiety-fear and satisfaction-like. *PLoS ONE*, 9(2), e87955.
- Fàbrega, E., Tibau, J., Soler, J., Fernández, J., Font, J., Carrión, D., Diestre, A., & Manteca, X. (2003). Feeding patterns, growth performance and carcass traits in group-housed growing-finishing pigs: the effect of terminal sire line, halothane genotype and age. *Animal Science*, 77(1), 11-22.
- Fernández, J., Fàbrega, E., Soler, J., Tibau, J., Ruiz, J.L., Puigvert, X., & Manteca, X. (2011). Feeding strategy in group-housed growing pigs of four different breeds. *Applied Animal Behaviour Science*, 134(3-4), 109-120.
- Fraser, D. (2008). Understanding animal welfare. *Acta Veterinaria Scandinavica*, 50(Suppl 1), S1.

- Giddings, B., Hopwood, B., & O'Brien, G. (2002). Environment, economy and society: fitting them together into sustainable development. *Sustainable Development*, 10(4), 187-196.
- Gjerde, I., & Wegge, P. (1987). Activity Patterns of Capercaillie, Tetrao urogallus, during Winter. *Holarctic Ecology*, 10(4), 286-293.
- Gonyou, H.W., Chapple, R.P., & Frank, G.R. (1992). Productivity, time budgets and social aspects of eating in pigs penned in groups of five or individually. *Applied Animal Behaviour Science*, 34(4), 291-301.
- Gregorini, P., Villalba, J.J., Provenza, F.D., Beukes, P.C., & Forbes, J.M. (2015). Modelling preference and diet selection patterns by grazing ruminants: a development in a mechanistic model of a grazing dairy cow, MINDY. *Animal Production Science*, 55(3), 360-375.
- Griffith, M.K., & Minton, J.E. (1991). Free-running rhythms of adrenocorticotrophic hormone (ACTH), cortisol and melatonin in pigs. *Domestic Animal Endocrinology*, 8(2), 201-208.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., & DeAngelis, D.L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, 198(1-2), 115-126.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., & Railsback, S.F. (2010). The ODD protocol: A review and first update. *Ecological Modelling*, 221(23), 2760-2768.
- Grimm, V., & Railsback, S. (2005). *Individual-based Modeling and Ecology: (Princeton Series in Theoretical and Computational Biology)*. Princeton, NJ: Princeton University Press.
- Grimm, V., & Railsback, S.F. (2012). Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 367(1586), 298-310.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., & DeAngelis, D.L. (2005). Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, 310(5750), 987-991.
- Grimm, V., Wyszomirski, T., Aikman, D., & Uchmański, J. (1999). Individual-based modelling and ecological theory: synthesis of a workshop. *Ecological Modelling*, 115(2-3), 275-282.
- Groenestein, C.M., Monteny, G.J., Aarnink, A.J.A., & Metz, J.H.M. (2007). Effect of urinations on the ammonia emission from group-housing systems for sows with straw bedding: Model assessment. *Biosystems Engineering*, 97(1), 89-98.
- Haefner, J.W. (2005). *Modeling biological systems: principles and applications*. New York, USA: Springer.
- Happe, K., Hutchings, N.J., Dalgaard, T., & Kellerman, K. (2011). Modelling the interactions between regional farming structure, nitrogen losses and environmental regulation. *Agricultural Systems*, 104(3), 281-291.
- Hemelrijk, C.K. (1999). An individual-orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1417), 361-369.

- Hemelrijk, C.K. (2000). Towards the integration of social dominance and spatial structure. *Animal Behaviour*, 59(5), 1035-1048.
- Hemelrijk, C.K., & Kunz, H. (2005). Density distribution and size sorting in fish schools: an individual-based model. *Behavioral Ecology*, 16(1), 178-187.
- Hemsworth, P.H., Rice, M., Nash, J., Giri, K., Butler, K.L., Tilbrook, A.J., & Morrison, R.S. (2013). Effects of group size and floor space allowance on grouped sows: Aggression, stress, skin injuries, and reproductive performance1. *Journal of Animal Science*, 91, 4953-4964.
- Herskin, M.S., & Jensen, K.H. (2000). Effects of different degrees of social isolation on the behaviour of weaned piglets kept for experimental purposes. *Animal Welfare*, 9(3), 237-249.
- Hessing, M.J.C., Schouten, W.G.P., Wiepkema, P.R., & Tielen, M.J.M. (1994). Implications of individual behavioural characteristics on performance in pigs. *Livestock Production Science*, 40(2), 187-196.
- Hildenbrandt, H., Carere, C., & Hemelrijk, C.K. (2010). Self-organized aerial displays of thousands of starlings: a model. *Behavioral Ecology*, 21(6), 1349-1359.
- Hillmann, E., Schrader, L., Mayer, C., & Gygas, L. (2008). Effects of weight, temperature and behaviour on the circadian rhythm of salivary cortisol in growing pigs. *Animal*, 2(03), 405-409.
- Hogan, J.A. (1997). Energy models of motivation: A reconsideration. *Applied Animal Behaviour Science*, 53(1-2), 89-105.
- Hogan, J.A., & van Boxel, F. (1993). Causal factors controlling dustbathing in Burmese red junglefowl: some results and a model. *Animal Behaviour*, 46(4), 627-635.
- Hoy, S., Schamun, S., & Weirich, C. (2012). Investigations on feed intake and social behaviour of fattening pigs fed at an electronic feeding station. *Applied Animal Behaviour Science*, 139(1), 58-64.
- Hughes, B.O., & Duncan, I.J.H. (1988). The notion of ethological 'need', models of motivation and animal welfare. *Animal Behaviour*, 36(6), 1696-1707.
- Hyun, Y., & Ellis, M. (2001). Effect of group size and feeder type on growth performance and feeding patterns in growing pigs. *Journal of Animal Science*, 79(4), 803-810.
- Hyun, Y., & Ellis, M. (2002). Effect of group size and feeder type on growth performance and feeding patterns in finishing pigs. *Journal of Animal Science*, 80(3), 568-574.
- Hyun, Y., Ellis, M., McKeith, F.K., & Wilson, E.R. (1997). Feed intake pattern of group-housed growing-finishing pigs monitored using a computerized feed intake recording system. *Journal of Animal Science*, 75(6), 1443-1451.
- Ilari-Antoine, E., Bonneau, M., Klauke, T.N., Gonzalez, J., Dourmad, J.Y., de Greef, K., Houwers, H.W., Fabrega, E., Zimmer, C., Hviid, M., Van der Oever, B., & Edwards, S.A. (2014). Evaluation of the sustainability of contrasted pig farming systems: economy. *Animal*, 8(12), 2047-2057.
- Illius, A.W., & Gordon, I.J. (1987). The allometry of food Intake in grazing ruminants. *Journal of Animal Ecology*, 56(3), 989-999.
- Ingram, D.L., & Dauncey, M.J. (1985). Circadian rhythms in the pig. *Comparative Biochemistry and Physiology. Part A: Physiology*, 82(1), 1-5.
- Jachowski, D.S., & Singh, N.J. (2015). Toward a mechanistic understanding of animal migration: incorporating physiological measurements in the study of animal movement. *Conservation Physiology*, 3(1).



- Janz, J.A.M., Morel, P.C.H., Wilkinson, B.H.P., & Purchas, R.W. (2007). Preliminary investigation of the effects of low-level dietary inclusion of fragrant essential oils and oleoresins on pig performance and pork quality. *Meat Science*, 75(2), 350-355.
- Jensen, P., & Toates, F.M. (1993). Who needs 'behavioural needs'? Motivational aspects of the needs of animals. *Applied Animal Behaviour Science*, 37(2), 161-181.
- Jensen, P., & Toates, F.M. (1997). Stress as a state of motivational systems. *Applied Animal Behaviour Science*, 53(1-2), 145-156.
- Johnson, A.W. (2013). Eating beyond metabolic need: how environmental cues influence feeding behavior. *Trends in Neurosciences*, 36(2), 101-109.
- Johnston, J.D. (2014). Physiological responses to food intake throughout the day. *Nutrition Research Reviews*, 27(1), 107-118.
- Kanis, E. (1990). Effect of food intake capacity on production traits in growing pigs with restricted feeding. *Animal Science*, 50(02), 333-341.
- Kanis, E., Groen, A., & de Greef, K. (2003). Societal concerns about pork and pork production and their relationships to the production system. *Journal of Agricultural and Environmental Ethics*, 16(2), 137-162.
- Keeling, L.J. (2005). Healthy and happy: animal welfare as an integral part of sustainable agriculture. *AMBIO: A Journal of the Human Environment*, 34(4), 316-319.
- Keeling, L.J., & Hurnik, J.F. (1996). Social facilitation acts more on the appetitive than the consummatory phase of feeding behaviour in domestic fowl. *Animal Behaviour*, 52(1), 11-15.
- Kirkden, R.D., & Pajor, E.A. (2006). Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. *Applied Animal Behaviour Science*, 100(1-2), 29-47.
- Koolhaas, J.M., Korte, S.M., de Boer, S.F., van Der Vegt, B.J., van Reenen, C.G., Hopster, H., de Jong, I.C., Ruis, M.A.W., & Blokhuis, H.J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, 23(7), 925-935.
- Koolhaas, J.M., & van Reenen, C.G. (2016). Animal behaviour and well-being symposium: Interaction between coping style/personality, stress, and welfare: Relevance for domestic farm animals1. *Journal of Animal Science*, 94(6), 2284-2296.
- Koopmans, S.J., van der Meulen, J., Dekker, R., Corbijn, H., & Mroz, Z. (2005). Diurnal rhythms in plasma cortisol, insulin, glucose, lactate and urea in pigs fed identical meals at 12-hourly intervals. *Physiology & Behavior*, 84(3), 497-503.
- Kriegsfeld, L.J., LeSauter, J., Hamada, T., Pitts, S.M., & Silver, R. (2002). 18 - Circadian Rhythms in the Endocrine System. In D. W. Pfaff, A. P. Arnold, S. E. Fahrbach, A. M. Etgen, & R. T. Rubin (Eds.), *Hormones, Brain and Behavior* (pp. 33-91). San Diego, USA: Academic Press.
- Krystallis, A., de Barcellos, M.D., Kügler, J.O., Verbeke, W., & Grunert, K.G. (2009). Attitudes of European citizens towards pig production systems. *Livestock Science*, 126(1-3), 46-56.
- Kumar Jha, P., Challet, E., & Kalsbeek, A. (2015). Circadian rhythms in glucose and lipid metabolism in nocturnal and diurnal mammals. *Molecular and Cellular Endocrinology*, 418, Part 1, 74-88.

- Kunz, H., & Hemelrijk, C.K. (2003). Artificial fish schools: collective effects of school size, body size, and body form. *Artificial Life*, 9(3), 237-253.
- Labroue, F., Gueblez, R., & Sellier, P. (1997). Genetic parameters of feeding behaviour and performance traits in group-housed Large White and French Landrace growing pigs. *Genetics Selection Evolution*, 29(4), 451 - 468.
- Lange, M., & Thulke, H.-H. (2016). Elucidating transmission parameters of African swine fever through wild boar carcasses by combining spatio-temporal notification data and agent-based modelling. *Stochastic Environmental Research and Risk Assessment*, 1-13.
- Laposky, A.D., Bass, J., Kohsaka, A., & Turek, F.W. (2008). Sleep and circadian rhythms: Key components in the regulation of energy metabolism. *FEBS Letters*, 582(1), 142-151.
- Larsen, M.L.V., Andersen, H.M.-L., & Pedersen, L.J. (2016). Can tail damage outbreaks in the pig be predicted by behavioural change? *The Veterinary Journal*, 209, 50-56.
- Lassen, J., Sandøe, P., & Forkman, B. (2006). Happy pigs are dirty! – conflicting perspectives on animal welfare. *Livestock Science*, 103(3), 221-230.
- Lawrence, A.B., & Terlouw, E. (1993). A review of behavioral factors involved in the development and continued performance of stereotypic behaviors in pigs. *Journal of Animal Science*, 71(10), 2815-2825.
- Lee, J.-S., Filatova, T., Ligmann-Zielinska, A., Hassani-Mahmoei, B., Stonedahl, F., Lorscheid, I., Voinov, A., Polhill, J.G., Sun, Z., & Parker, D.C. (2015). The complexities of agent-based modeling output analysis. *Journal of Artificial Societies and Social Simulation*, 18(4), 4.
- Leiber-Schotte, C. (2009). *Einfluss der Rangordnung bei Jungebern im Eigenleistungstest auf Futteraufnahme und Futteraufnahmeverhalten unter Berücksichtigung endokrinologischer und immunologischer Parameter*. (PhD thesis), University of Veterinary Medicine, Hannover, Germany.
- Lewis, C.R.G., & McGlone, J.J. (2008). Modelling feeding behaviour, rate of feed passage and daily feeding cycles, as possible causes of fatigued pigs. *Animal*, 2(4), 600-605.
- Lewy, A.J., Tetsuo, M., Markey, S., Goodwin, F.K., & Kopin, I. (1980). Pinealectomy abolishes plasma melatonin in the rat. *Journal of Clinical Endocrinology and Metabolism*, 50(1), 204-205.
- Lindberg, A.C. (2001). Group Life. In L. J. Keeling & H. W. Gonyou (Eds.), *Social behavior in farm animals* (pp. 37-58). Wallingford, UK: CAB International.
- Lorenz, K.Z. (1950). The comparative method in studying innate behavior patterns. *Symposia of the Society for Experimental Biology*, 221-268.
- Lyons, C.A.P., Bruce, J.M., Fowler, V.R., & English, P.R. (1995). A comparison of productivity and welfare of growing pigs in four intensive systems. *Livestock Production Science*, 43(3), 265-274.
- Mackenzie, S.G., Leinonen, I., Ferguson, N., & Kyriazakis, I. (2016). Can the environmental impact of pig systems be reduced by utilising co-products as feed? *Journal of Cleaner Production*, 115, 172-181.
- Maljaars, J., Peters, H.P.F., & Masclee, A.M. (2007). Review article: the gastrointestinal tract: neuroendocrine regulation of satiety and food intake. *Alimentary Pharmacology and Therapeutics*, 26, 241-250.

- Mamlöf, K., Örberg, J., Hellberg, S., Cortova, Z., & Björkgren, S. (1990). The diurnal influence on utilization of dietary protein in the growing pig. *Journal of Animal Physiology and Animal Nutrition*, 63(1-5), 180-187.
- Maselyne, J., Saeys, W., & Van Nuffel, A. (2015). Review: Quantifying animal feeding behaviour with a focus on pigs. *Physiology & Behavior*, 138(0), 37-51.
- Mason, G., & Bateson, M. (2009). Motivation and the organization of behaviour, 2nd edn. *The Ethology of Domesticated Animals* (pp. 38-56). Wallingford, UK: CAB International.
- Mason, G., & Mendl, M. (1993). Why is there no simple way of measuring animal welfare? *Animal Welfare*, 2(4), 301-319.
- Matthews, S.G., Miller, A.L., Clapp, J., Plötz, T., & Kyriazakis, I. (2016). Early detection of health and welfare compromises through automated detection of behavioural changes in pigs. *The Veterinary Journal*, 217, 43-51.
- McFarland, D.J., & Sibly, R.M. (1975). The behavioural final common path. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 270(907), 265-293.
- McPhee, M.E., & Carlstead, K. (2010). The importance of maintaining natural behaviors in captive mammals. In D. G. Kleiman, K. V. Thompson, & C. K. Baer (Eds.), *Wild mammals in captivity: principles and techniques for zoo management* (pp. 303-313). USA: University of Chicago Press
- Mench, J. (1998). Why it is important to understand animal behavior. *ILAR Journal*, 39(1), 20-26.
- Miele, M., Blokhuis, H., Bennett, R., & Bock, B. (2013). Changes in farming and in stakeholder concern for animal welfare. In H. Blokhuis, M. Miele, I. Veissier, & B. Jones (Eds.), *Improving farm animal welfare: Science and society working together: the Welfare Quality approach* (pp. 19-47). Wageningen, the Netherlands: Wageningen Academic Publishers.
- Miller, E., & Ullrey, D. (1987). The pig as a model for human nutrition. *Annual Review of Nutrition*, 7(1), 361-382.
- Minton, J.E., Davis, D.L., & Stevenson, J.S. (1989). Contribution of the photoperiod to circadian variations in serum cortisol and melatonin in boars. *Domestic Animal Endocrinology*, 6(2), 177-181.
- Moinard, C., Mendl, M., Nicol, C.J., & Green, L.E. (2003). A case control study of on-farm risk factors for tail biting in pigs. *Applied Animal Behaviour Science*, 81(4), 333-355.
- Morgan, C.A., Emmans, G.C., Tolkamp, B.J., & Kyriazakis, I. (2000). Analysis of the feeding behavior of pigs using different models. *Physiology & Behavior*, 68(3), 395-403.
- Moughan, P.J. (1995). Modelling protein metabolism in the pig - first principles. In P. J. Moughan, M. W. A. Verstegen, & M. I. Visser-Reyneveld (Eds.), *Modelling growth in the pig* (pp. 59-70). Wageningen, the Netherlands: Wageningen Pers.
- Munsterhjelm, C., Brunberg, E., Heinonen, M., Keeling, L., & Valros, A. (2013a). Stress measures in tail biters and bitten pigs in a matched case-control study. *Animal Welfare*, 22(3), 331-338.
- Munsterhjelm, C., Heinonen, M., & Valros, A. (2016). Can tail-in-mouth behaviour in weaned piglets be predicted by behaviour and performance? *Applied Animal Behaviour Science*, 184, 16-24.

- Munsterhjelm, C., Simola, O., Keeling, L., Valros, A., & Heinonen, M. (2013b). Health parameters in tail biters and bitten pigs in a case-control study. *Animal*, 7(05), 814-821.
- Nelson, R.J. (2011). Homeostasis and behavior. In R. J. Nelson (Ed.), *An introduction to behavioral endocrinology* (pp. 453-510). Sunderland, MA, USA: Sinauer Associates.
- Nielsen, B.L. (1999). On the interpretation of feeding behaviour measures and the use of feeding rate as an indicator of social constraint. *Applied Animal Behaviour Science*, 63(1), 79-91.
- Nielsen, B.L., de Jong, I.C., & de Vries, T.J. (2016). The use of feeding behaviour in the assessment of animal welfare. In C. J. C. Phillips (Ed.), *Nutrition and the welfare of farm animals* (pp. 59-84). Switzerland: Springer International Publishing.
- Nielsen, B.L., Lawrence, A.B., & Whittemore, C.T. (1995). Effect of group size on feeding behaviour, social behaviour, and performance of growing pigs using single-space feeders. *Livestock Production Science*, 44(1), 73-85.
- Nielsen, B.L., Lawrence, A.B., & Whittemore, C.T. (1996a). Effect of individual housing on the feeding behaviour of previously group housed growing pigs. *Applied Animal Behaviour Science*, 47(3-4), 149-161.
- Nielsen, B.L., Lawrence, A.B., & Whittemore, C.T. (1996b). Feeding behaviour of growing pigs using single or multi-space feeders. *Applied Animal Behaviour Science*, 47(3-4), 235-246.
- Nienaber, J.A., McDonald, T.P., Hahn, G.L., & Chen, Y.R. (1990). Eating dynamics of growing-finishing swine. *Transactions of the ASAE*, 33(6), 2011-2018.
- Noblet, J., Shi, X.S., & Dubois, S. (1993). Energy cost of standing activity in sows. *Livestock Production Science*, 34(1), 127-136.
- NRC. (2012). *Nutrient requirements of swine*. Washington, D.C, USA: National Academies Press.
- Nyachoti, C.M., Zijlstra, R.T., de Lange, C.F.M., & Patience, J.F. (2004). Voluntary feed intake in growing-finishing pigs: A review of the main determining factors and potential approaches for accurate predictions. *Canadian Journal of Animal Science*, 84(4), 549-566.
- Ozaki, Y., & Lynch, H.J. (1976). Presence of melatonin in plasma and urine of pinealectomized rats. *Endocrinology*, 99(2), 641-644.
- Paterson, A., Martin, G., Foldes, A., Maxwell, C., & Pearce, G. (1992). Concentrations of plasma melatonin and luteinizing hormone in domestic gilts reared under artificial long or short days. *Journal of Reproduction and Fertility*, 94(1), 85-95.
- Payne, R.J.H., & Pagel, M. (1996). Escalation and time costs in displays of endurance. *Journal of Theoretical Biology*, 183(2), 185-193.
- Peckett, A.J., Wright, D.C., & Riddell, M.C. (2011). The effects of glucocorticoids on adipose tissue lipid metabolism. *Metabolism*, 60(11), 1500-1510.
- Pedersen, L.J., Jensen, M.B., Hansen, S.W., Munksgaard, L., Ladewig, J., & Matthews, L. (2002). Social isolation affects the motivation to work for food and straw in pigs as measured by operant conditioning techniques. *Applied Animal Behaviour Science*, 77(4), 295-309.
- Pettigrew, J.E. (2016). Essential role for simulation models in animal research and application. *Animal Production Science*.

- Price, E.O. (1999). Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science*, 65(3), 245-271.
- Puga-Gonzalez, I., Hildenbrandt, H., & Hemelrijk, C.K. (2009). Emergent patterns of social affiliation in primates, a model. *PLoS Computational Biology*, 5(12), e1000630.
- Puga-Gonzalez, I., Hoscheid, A., & Hemelrijk, C.K. (2015). Friendship, reciprocation, and interchange in an individual-based model. *Behavioral Ecology and Sociobiology*, 69(3), 383-394.
- Puppe, B., Ernst, K., Schön, P.C., & Manteuffel, G. (2007). Cognitive enrichment affects behavioural reactivity in domestic pigs. *Applied Animal Behaviour Science*, 105(1), 75-86.
- Quiniou, N., Dourmad, J.-Y., & Noblet, J. (1996). Effect of energy intake on the performance of different types of pig from 45 to 100 kg body weight. 1. Protein and lipid deposition. *Animal Science*, 63(02), 277-288.
- Quiniou, N., Dubois, S., & Noblet, J. (2000). Voluntary feed intake and feeding behaviour of group-housed growing pigs are affected by ambient temperature and body weight. *Livestock Production Science*, 63(3), 245-253.
- R Core Team. (2015). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>
- Railsback, S.F., & Grimm, V. (2012). *Agent-based and individual-based modeling: a practical introduction*. Princeton, New Jersey: Princeton University Press.
- Rangel-Huerta, A., & Muñoz-Meléndez, A. (2010). Kinetic theory of situated agents applied to pedestrian flow in a corridor. *Physica A: Statistical Mechanics and its Applications*, 389(5), 1077-1089.
- Rauw, W.M., Soler, J., Tibau, J., Reixach, J., & Gomez Raya, L. (2006). Feeding time and feeding rate and its relationship with feed intake, feed efficiency, growth rate, and rate of fat deposition in growing Duroc barrows. *Journal of Animal Science*, 84(12), 3404-3409.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., & Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291-318.
- Reilly, T., & Waterhouse, J. (2007). Altered sleep-wake cycles and food intake: The Ramadan model. *Physiology & Behavior*, 90(2-3), 219-228.
- Rosenwasser, A.M., Boulous, Z., & Terman, M. (1981). Circadian organization of food intake and meal patterns in the rat. *Physiology & Behavior*, 27(1), 33-39.
- Ruis, M.A.W., te Brake, J.H.A., Engel, B., Buist, W.G., Blokhuis, H.J., & Koolhaas, J.M. (2001). Adaptation to social isolation: Acute and long-term stress responses of growing gilts with different coping characteristics. *Physiology & Behavior*, 73(4), 541-551.
- Ruis, M.A.W., te Brake, J.H.A., Engel, B., Ekkel, E.D., Buist, W.G., Blokhuis, H.J., & Koolhaas, J.M. (1997). The circadian rhythm of salivary cortisol in growing pigs: effects of age, gender, and stress. *Physiology & Behavior*, 62(3), 623-630.
- Rushen, J., Chapinal, N., & de Passillé, A.M. (2012). Automated monitoring of behavioural-based animal welfare indicators. *Animal Welfare-The UFAW Journal*, 21(3), 339.
- Rushen, J., & de Passillé, A.M. (2009). The scientific basis of animal welfare indicators. *Food Safety Assurance and Veterinary Public Health*, 5, 391-416.

- Salfen, B., Carroll, J., & Keisler, D. (2003). Endocrine responses to short-term feed deprivation in weanling pigs. *Journal of Endocrinology*, 178(3), 541-551.
- Sauvant, D., Baumont, R., & Faverdin, P. (1996). Development of a mechanistic model of intake and chewing activities of sheep. *Journal of Animal Science*, 74(11), 2785-2802.
- Scheer, F.A.J.L., Morris, C.J., & Shea, S.A. (2013). The internal circadian clock increases hunger and appetite in the evening independent of food intake and other behaviors. *Obesity*, 21(3), 421-423.
- Schodl, K., Klein, F., & Winckler, C. (2017). Mapping sustainability in pig farming research using keyword network analysis. *Livestock Science*, 196, 28-35.
- Schouten, W.G.P. (1986). *Rearing conditions and behaviour in pigs*. (PhD thesis), Wageningen University, Wageningen, the Netherlands.
- Schrenk, H.J. (1981). *Der Einfluss von Licht und Futtergabe auf den Tagesrhythmus der Aktivitaet von Ferkeln*. (PhD thesis), Universitaet Hohenheim, Stuttgart, Germany.
- Schrøder-Petersen, D.L., & Simonsen, H.B. (2001). Tail biting in pigs. *The Veterinary Journal*, 162(3), 196-210.
- Schwartz, M.W., Woods, S.C., Seeley, R.J., Barsh, G.S., Baskin, D.G., & Leibel, R.L. (2003). Is the energy homeostasis system inherently biased toward weight gain? *Diabetes*, 52(2), 232-238.
- Scott, K., Chennells, D.J., Campbell, F.M., Hunt, B., Armstrong, D., Taylor, L., Gill, B.P., & Edwards, S.A. (2006). The welfare of finishing pigs in two contrasting housing systems: Fully-slatted versus straw-bedded accommodation. *Livestock Science*, 103(1-2), 104-115.
- Scrimgeour, K., Gresham, M.J., Giles, L.R., Thomson, P.C., Wynn, P.C., & Newman, R.E. (2008). Ghrelin secretion is more closely aligned to energy balance than with feeding behaviour in the grower pig. *Journal of Endocrinology*, 198(1), 135-145.
- Sih, A., Bell, A., & Johnson, J.C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, 19(7), 372-378.
- Smith, J.M., & Parker, G.A. (1976). The logic of asymmetric contests. *Animal Behaviour*, 24(1), 159-175.
- Smith, J.M., & Price, G.R. (1973). The logic of animal conflict. *Nature*, 246, 15-18.
- Smulders, D., Verbeke, G., Mormède, P., & Geers, R. (2006). Validation of a behavioral observation tool to assess pig welfare. *Physiology & Behavior*, 89(3), 438-447.
- Sørensen, L.B., Møller, P., Flint, A., Martens, M., & Raben, A. (2003). Effect of sensory perception of foods on appetite and food intake: a review of studies on humans. *International Journal of Obesity*, 27(10), 1152-1166.
- Spoolder, H., Schöne, M., & Bracke, M. (2016). Initiatives to reduce mutilations in EU livestock production: Wageningen UR Livestock Research.
- Statham, P., Green, L., Bichard, M., & Mendl, M. (2009). Predicting tail-biting from behaviour of pigs prior to outbreaks. *Applied Animal Behaviour Science*, 121(3-4), 157-164.
- Steinfeld, H., Gerber, P., Wassenaar, T., Castel, V., & de Haan, C. (2006). *Livestock's long shadow: environmental issues and options*. Rome, Italy: FAO.
- Stern, S., Sonesson, U., Gunnarsson, S., Öborn, I., Kumm, K.-I., & Nybrant, T. (2005). Sustainable development of food production: a case study on scenarios for pig production. *Ambio*, 34(4), 402-407.

- Stolba, A., & Wood-Gush, D.G.M. (1980). Arousal and exploration in growing pigs in different environments. *Applied Animal Ethology*, 6(4), 382-383.
- Strathe, A.B., Danfær, A., & Chwalibog, A. (2008). A dynamic model of digestion and absorption in pigs. *Animal Feed Science and Technology*, 143(1-4), 328-371.
- Stricker, E.M., & Verbalis, J.G.C. (1988). Hormones and behavior: the biology of thirst and sodium appetite. *American Scientist*, 76(3), 261-267.
- Stricklin, W.R., de Bourcier, P., Zhou, J.Z., & Gonyou, H.W. (1998). Artificial pigs in space: using artificial intelligence and artificial life techniques to design animal housing. *Journal of Animal Science*, 76(10), 2609-2613.
- Stricklin, W.R., Zhou, J.Z., & Gonyou, H.W. (1995). Selfish animats and robot ethology: using artificial animals to investigate social and spatial behavior. *Applied Animal Behaviour Science*, 44(2-4), 187-203.
- Strubbe, J.H., & van Dijk, G. (2002). The temporal organization of ingestive behaviour and its interaction with regulation of energy balance. *Neuroscience & Biobehavioral Reviews*, 26(4), 485-498.
- Studnitz, M., Jensen, M.B., & Pedersen, L.J. (2007). Why do pigs root and in what will they root?: A review on the exploratory behaviour of pigs in relation to environmental enrichment. *Applied Animal Behaviour Science*, 107(3-4), 183-197.
- Sutherland, M., Davis, B., & McGlone, J. (2011). The effect of local or general anesthesia on the physiology and behavior of tail docked pigs. *Animal*, 5(8), 1237-1246.
- Szendrő, K., Szendrő, Z., Matics, Z., Dalle Zotte, A., Odermatt, M., Radnai, I., & Gerencsér, Z. (2015). Effect of genotype, housing system and hay supplementation on performance and ear lesions of growing rabbits. *Livestock Science*, 174, 105-112.
- Tast, A., Love, R.J., Evans, G., Andersson, H., Peltoniemi, O.A.T., & Kennaway, D.J. (2001a). The photophase light intensity does not affect the scotophase melatonin response in the domestic pig. *Animal Reproduction Science*, 65(3-4), 283-290.
- Tast, A., Love, R.J., Evans, G., Telsfer, S., Giles, R., Nicholls, P., Voultsios, A., & Kennaway, D.J. (2001b). The pattern of melatonin secretion is rhythmic in the domestic pig and responds rapidly to changes in daylength. *Journal of Pineal Research*, 31(4), 294-300.
- Taylor, N.R., Main, D.C.J., Mendl, M., & Edwards, S.A. (2010). Tail-biting: A new perspective. *The Veterinary Journal*, 186(2), 137-147.
- Taylor, N.R., Parker, R.M.A., Mendl, M., Edwards, S.A., & Main, D.C.J. (2012). Prevalence of risk factors for tail biting on commercial farms and intervention strategies. *The Veterinary Journal*, 194(1), 77-83.
- Temple, D., Manteca, X., Velarde, A., & Dalmau, A. (2011). Assessment of animal welfare through behavioural parameters in Iberian pigs in intensive and extensive conditions. *Applied Animal Behaviour Science*, 131(1-2), 29-39.
- Ten Broeke, G., van Voorn, G., & Ligtenberg, A. (2016). Which Sensitivity Analysis Method Should I Use for My Agent-Based Model? *Journal of Artificial Societies and Social Simulation*, 19(1), 5.
- Thingnes, S.L., Ekker, A.S., Gaustad, A.H., & Framstad, T. (2012). Ad libitum versus step-up feeding during late lactation: The effect on feed consumption, body composition and production performance in dry fed loose housed sows. *Livestock Science*, 149(3), 250-259.

- Thomassen, M.A., Dolman, M.A., van Calker, K.J., & de Boer, I.J.M. (2009). Relating life cycle assessment indicators to gross value added for Dutch dairy farms. *Ecological Economics*, 68(8-9), 2278-2284.
- Thorslund, C.A.H., Aaslyng, M.D., & Lassen, J. (2017). Perceived importance and responsibility for market-driven pig welfare: Literature review. *Meat Science*, 125, 37-45.
- Tichit, M., Puillet, L., & Sauvant, D. (2009). How models contribute to livestock farming system research: overview of recent advances. *Options Méd*, 293-306.
- Tucker, C., Mench, J., von Keyserlingk, M., & Kebreab, E. (2013). Animal welfare: an integral component of sustainability. *Sustainable Animal Agriculture*. Wallingford: CAB International, 42-52.
- Ursinus, W.W., van Reenen, C.G., Kemp, B., & Bolhuis, J.E. (2014). Tail biting behaviour and tail damage in pigs and the relationship with general behaviour: Predicting the inevitable? *Applied Animal Behaviour Science*, 156, 22-36.
- Van Calker, K.J., Berentsen, P.B.M., de Boer, I.M.J., Giesen, G.W.J., & Huirne, R.B.M. (2004). An LP-model to analyse economic and ecological sustainability on Dutch dairy farms: model presentation and application for experimental farm "de Marke". *Agricultural Systems*, 82(2), 139-160.
- Van de Weerd, H.A., & Day, J.E.L. (2009). A review of environmental enrichment for pigs housed in intensive housing systems. *Applied Animal Behaviour Science*, 116(1), 1-20.
- Van de Weerd, H.A., Docking, C.M., Day, J.E.L., Breuer, K., & Edwards, S.A. (2006). Effects of species-relevant environmental enrichment on the behaviour and productivity of finishing pigs. *Applied Animal Behaviour Science*, 99(3-4), 230-247.
- Van Milgen, J., Bernier, J.F., Lecoq, Y., Dubois, S., & Noblet, J. (1998). Major determinants of fasting heat production and energetic cost of activity in growing pigs of different body weight and breed/castration combination. *British Journal of Nutrition*, 79(06), 509-517.
- Vanderelst, D., Ahn, R.M.C., & Barakova, E.I. (2009). Simulated Trust: A cheap social learning strategy. *Theoretical Population Biology*, 76(3), 189-196.
- Velarde, A., Fàbrega, E., Blanco-Penedo, I., & Dalmau, A. (2015). Animal welfare towards sustainability in pork meat production. *Meat Science*, 109, 13-17.
- Vera, F., Zenuto, R.R., & Antenucci, C.D. (2012). Differential responses of cortisol and corticosterone to adrenocorticotrophic hormone (ACTH) in a subterranean rodent (*Ctenomys talarum*). *Journal of Experimental Zoology. Part A: Ecological Genetics and Physiology*, 317(3), 173-184.
- Vermeer, H.M., de Greef, K.H., & Houwers, H.W.J. (2014). Space allowance and pen size affect welfare indicators and performance of growing pigs under Comfort Class conditions. *Livestock Science*, 159, 79-86.
- Verstegen, M.W.A., van der Hel, W., Brandsma, H.A., Henken, A.M., Kanis, E., & van der Wal, P. (1991). Effects of recombinant porcine somatotropin on metabolic rate in growing pigs. *Journal of Animal Science*, 69(7), 2961-2970.
- Walker, N. (1991). The effects on performance and behaviour of number of growing pigs per mono-place feeder. *Animal Feed Science and Technology*, 35(1-2), 3-13.



- Wallenbeck, A., & Keeling, L.J. (2013). Using data from electronic feeders on visit frequency and feed consumption to indicate tail biting outbreaks in commercial pig production. *Journal of Animal Science*, 91(6), 2879-2884.
- Welfare Quality®. (2009). Welfare Quality® Assessment Protocol for Pigs (sows and piglets, growing and finishing pigs). *Welfare Quality Consortium, Lelystad, the Netherlands*.
- Wellock, I.J., Emmans, G.C., & Kyriazakis, I. (2003). Predicting the consequences of social stressors on pig food intake and performance. *Journal of Animal Science*, 81(12), 2995-3007.
- Wellock, I.J., Emmans, G.C., & Kyriazakis, I. (2004). Modeling the effects of stressors on the performance of populations of pigs. *Journal of Animal Science*, 82(8), 2442-2450.
- Wenk, C. (2001). The role of dietary fibre in the digestive physiology of the pig. *Animal Feed Science and Technology*, 90(1-2), 21-33.
- Wheelhouse, R.K., & Hacker, R.R. (1982). The effect of four different types of fluorescent light on growth, reproductive performance, pineal weight and retinal morphology of Yorkshire gilts. *Canadian Journal of Animal Science*, 62(2), 417-424.
- Wiepkema, P.R., & Koolhaas, J.M. (1993). Stress and Animal Welfare. *Animal Welfare*, 2(3), 195-218.
- Wilensky, U. (1999). Netlogo. Retrieved 18 November 2013, 2013, from <http://ccl.northwestern.edu/netlogo/>
- Willems, J., van Grinsven, H.J.M., Jacobsen, B.H., Jensen, T., Dalgaard, T., Westhoek, H., & Kristensen, I.S. (2016). Why Danish pig farms have far more land and pigs than Dutch farms? Implications for feed supply, manure recycling and production costs. *Agricultural Systems*, 144, 122-132.
- Williams, N.H., Stahly, T.S., & Zimmerman, D.R. (1997). Effect of level of chronic immune system activation on the growth and dietary lysine needs of pigs fed from 6 to 112 kg. *Journal of Animal Science*, 75(9), 2481-2496.
- Wolf, M., & Weissing, F.J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3959-3968.
- Woods, S.C., & D'Alessio, D.A. (2008). Central Control of Body Weight and Appetite. *Journal of Clinical Endocrinology & Metabolism*, 93(11 supplement 1), s37-s50.
- Yeates, J.W., & Main, D.C.J. (2008). Assessment of positive welfare: A review. *The Veterinary Journal*, 175(3), 293-300.
- Yoosuk, S., Ong, H.B., Roan, S.W., Morgan, C.A., & Whittemore, C.T. (2011). A simulation model for predicting the voluntary feed intake of a growing pig. *Acta Agriculturae Scandinavica Section A Animal Science*, 61(4), 168-186.
- Young, R.J., & Lawrence, A.B. (1994). Feeding behaviour of pigs in groups monitored by a computerized feeding system. *Animal Science*, 58(01), 145-152.
- Zonderland, J.J. (2010). *Talking tails : quantifying the development of tail biting in pigs*. (PhD thesis), Wageningen University, Wageningen, the Netherlands.
- Zonderland, J.J., Kemp, B., Bracke, M.B.M., den Hartog, L.A., & Spoolder, H.A.M. (2011a). Individual piglets contribution to the development of tail biting. *Animal*, 5(4), 601-607.

- Zonderland, J.J., Schepers, F., Bracke, M.B.M., den Hartog, L.A., Kemp, B., & Spoolder, H.A.M. (2011b). Characteristics of biter and victim piglets apparent before a tail-biting outbreak. *Animal*, 5(5), 767-775.
- Zupan, M., Janczak, A.M., Framstad, T., & Zanella, A.J. (2012). The effect of biting tails and having tails bitten in pigs. *Physiology & Behavior*, 106(5), 638-644.





# Summary

The transition towards sustainable pig production systems is receiving increasing attention nowadays. Sustainability is a multidimensional concept that includes many environmental, economic and societal issues. To be able to make conscious decisions for desired developments of pig production systems, we need to understand trade-offs and synergies between sustainability issues.

Pig behaviour plays a central role in sustainability, as it is an important indicator for pig welfare and can also affect other sustainability issues. Understanding behaviour and related welfare consequences requires to understand motivations underlying behaviour. Modelling studies can help in understanding relations between behaviour and welfare. So far, however, studies focussed either on understanding animal behaviour and underlying motivations, or on evaluating or predicting animal welfare at farm level without understanding motivations underlying behaviour.

The two aims of this thesis were: 1) to assess the use of agent-based modelling for understanding pig behaviour and underlying motivations, and 2) to apply agent-based modelling for increasing our understanding of pig behaviour, and related animal welfare and productivity performance.

The use of agent-based modelling for understanding pig behaviour and underlying motivation was explored with a case study of tail biting behaviour. In pig production, tail biting behaviour is considered to be a major welfare issue with a large impact on the profitability of a farm. An agent-based model was developed to understand the causation of tail biting behaviour. Pigs in the model started as neutral pigs (not involved in biting incidents), but could change into a biter, victim, or both biter and victim. Tail biting behaviour could emerge when pigs were unable to fulfil their internal motivation to explore. The effects of a redirected exploratory motivation, behavioural changes in victims and preference to bite a lying pig on tail biting patterns were tested in our model. Model results show that redirected motivation of explorative behaviour can cause tail biting behaviour, and that the incidence of tail biting between groups can vary by chance. Preference to bite a lying pig and an effect of biting on the behavioural motivations of a victim were of minor importance in this incidence. The behavioural time budget of a pig, however, might be important in predisposing pigs to or preventing them from becoming involved in biting incidents.

Since the causation of tail biting behaviour is not understood well enough to further develop a model that enables animal welfare and productivity assessment, we continued with studying feeding behaviour. To gain more understanding of feeding behaviour and internal (physiological) factors, a mechanistic and dynamic simulation model was developed. This model included motivations underlying feeding behaviour

and various feeding patterns of an individually housed growing pig. The model integrates knowledge from physiology and ethology, and combines growth with a behavioural decision model based on motivation. Interaction between growth and motivation led to emergent feeding behaviour, which allowed exploring the development of a pig over time, in particular the causation of growth and feeding patterns during the entire growing period. Physiological factors, affected by pig and feed characteristics, are important internal factors controlling feeding behaviour. Model output included short-term feeding behaviours in pigs (e.g. meal size, meal frequency and meal duration), and growth characteristics (e.g. energy use, body weight gain). The model yielded feeding patterns that were validated against empirical data. This model explains the change in feeding motivation and behaviour of pigs during the entire growth and fattening period from about 25 to 130 kg body weight. Moreover, this model enables understanding of the importance of physiological factors, and pig and diet characteristics underlying feeding motivation.

Pigs show an alternans feeding pattern, that is, a small peak of feed intake at the beginning of the day and a larger peak at the end of the day. To deepen our understanding of mechanisms underlying this feeding pattern within 24 hours, we included hormonal circadian rhythms in the model. The model contains mechanisms that regulate feeding behaviour of animals, including: processing of feed in the gastrointestinal tract, fluctuation in energy balance, circadian rhythms of melatonin and cortisol and motivational decision-making. From the interactions between these various processes, feeding patterns (e.g. feed intake, meal frequency, feeding rate) within 24 hours emerge. These feeding patterns, as well as patterns for the underlying mechanisms (e.g. energy expenditure), fitted empirical data well, indicating that our model contains relevant mechanisms. The circadian rhythms of cortisol and melatonin explained the alternans pattern of feeding in pigs. Additionally, the timing and amplitude of cortisol peaks affected the diurnal and nocturnal peaks in feed intake. Model results indicate that the hormones melatonin and cortisol directly drive energy metabolism affecting feeding behaviour, whereas other hormones, such as leptin and ghrelin, regulate feeding behaviour depending on the energy status of the animal.

In a next step, an agent-based model of feeding and social interaction in pigs was developed to simulate feeding behaviour of commercially group-housed pigs. In this model, multiple pigs and social factors were included in the model to increase our understanding of the complex interaction between internal physiological factors and external social factors. Animals living in groups compete for food resources and face social food conflicts. Social factors (e.g. competition level and social facilitation) and behavioural strategies (e.g. avoidance and approach) affected social interactions among pigs and feeding behaviour. Model results show that feeding patterns, especially feeding time, can affect competition and cause conflicts for feed in group-housed pigs. Beyond a certain point of competition, meal-based (e.g. meal frequency

and size) and social interaction patterns (e.g. avoidance and displacements) are determined mainly by behavioural strategies. The average daily feeding time can be used to predict the group size at which this turning point occurs. Model results show that social facilitation is less important, although it can increase competition between pigs. Changed feeding patterns, such as meal frequency, feeding rate, and feeder occupation during day and night, are promising indicators for animal welfare in pig production systems at group level.

Next, the agent-based model of feeding and social interaction was used to understand how pig characteristics affect variation in feeding, social interaction and growth patterns among group-housed pigs. Variation in feeding, interaction and growth patterns among pigs can be explained by variation in pig characteristics that, on the one hand, affect physiological factors and, on the other hand, behavioural strategies to approach or avoid conflicts at the feeder. Model results show that pig characteristics, such as growth potential and dominance rank, affect behaviour and growth patterns. Furthermore, they can affect abilities of pigs to cope with social constraints that inhibit them from feeding when they want to, for example, when other pigs use the feeder. Individual variation in behavioural strategies can reduce aggression at group level, but can make individual pigs more susceptible to social constraints. Feeding patterns, such as feeding rate or meal frequency, should be interpreted differently in relation to animal welfare at group level or at individual level. We suggest that a combination of feeding patterns, such as feed intake, feeding time and meal frequency, is more suitable for identifying pigs with welfare risks within a group.

Agent-based modelling was applied for increasing our understanding of pig behaviour and related animal welfare and productivity performance. The model includes measurements that can indicate welfare issues, such as number of conflicts, received displacements, number of interactions won or lost, and level of feeding motivation (hunger). It also includes measurements that can indicate productivity, such as body weight gain (in protein and fat deposition) and feed conversion ratio. The model, therefore, can be used to analyse trade-offs and synergies between behaviours and growth performance under different conditions, such as various group sizes, and homogeneous versus heterogeneous groups (e.g. in growth potential, body weight and coping style).

In conclusion, agent-based modelling proved to be a useful method to understand animal behaviour and underlying motivations. It contributed to further understanding of tail biting and feeding behaviour in pigs in all its complexity. Furthermore, agent-based modelling showed to be a novel method to find and assess behavioural indicators for animal welfare, and to contribute to understanding trade-offs and synergies between sustainability issues, such as animal welfare and productivity.





# Samenvatting

De overgang naar duurzame varkensproductiesystemen krijgt tegenwoordig steeds meer aandacht. Duurzaamheid is een multidimensionaal concept dat milieu-, economische en maatschappelijke aspecten omvat. Om bewuste beslissingen te kunnen maken voor de gewenste ontwikkeling van varkensproductiesystemen, is het belangrijk dat we trade-offs en synergiën tussen duurzaamheidsaspecten kennen.

Varkensgedrag speelt een centrale rol in duurzaamheid, aangezien het een belangrijke indicator voor varkenswelzijn is en ook andere aspecten van duurzaamheid kan beïnvloeden. Voor het begrijpen van gedrag en de gevolgen voor welzijn, is het essentieel dat de motivaties onderliggend aan het gedrag worden begrepen. Modelleren kan bijdragen aan het begrijpen van relaties tussen gedrag en welzijn. Tot op heden hebben modelleerstudies zich vooral gericht op het begrijpen van diergedrag en onderliggende motivaties, of op het beoordelen of voorspellen van dierenwelzijn op bedrijfsniveau zonder de onderliggende motivaties van gedrag hierin mee te nemen.

De twee doelen van het onderzoek in dit proefschrift waren: 1) het beoordelen van het gebruik van individu-gebaseerde modellen om varkensgedrag en de onderliggende motivatie te begrijpen, en 2) het toepassen van deze modelleermethode om meer inzicht te krijgen in varkensgedrag, gerelateerd dierenwelzijn en productiviteit.

Het gebruik van individu-gebaseerde modellen om varkensgedrag en onderliggende motivatie te begrijpen is onderzocht met een casus over staartbijtgedrag. Staartbijten wordt gezien als een groot probleem in de varkenshouderij met betrekking tot negatieve effecten op dierenwelzijn en winstgevendheid van een bedrijf. Een individu-gebaseerd model is ontwikkeld om de oorzaak van staartbijten te begrijpen. De varkens in het model begonnen als neutrale varkens (niet betrokken bij bijtincidenten), maar konden veranderen in een bijter, slachtoffer, of zowel bijter als slachtoffer. Staartbijtgedrag kon zich voordoen wanneer varkens hun interne motivatie om hun omgeving te exploreren niet konden uitvoeren. Effecten van omgerichte motivatie tot exploreren, gedragsveranderingen in slachtoffers en een voorkeur om een liggend varken te bijten zijn getest in het model. De resultaten laten zien dat omgerichte motivatie tot exploreren staartbijtgedrag kan veroorzaken en dat de hoeveelheid staartbijtgevallen door toeval per groep kan variëren. Gedragsveranderingen in slachtoffers en een voorkeur om een liggend varken te bijten hadden weinig effect op het voorkomen van staartbijten. De tijdsbesteding van een varken kan een belangrijke factor zijn in de ontvankelijkheid van een varken om een bijter te worden of bij een bijtincident betrokken te raken.

Aangezien de oorzaak van staartbijtgedrag niet goed genoeg begrepen wordt om dit gedrag verder te kunnen modelleren in relatie tot dierenwelzijn en productiviteit, richtte de vervolgstudie zich op eetgedrag. We hebben een mechanistisch en dynamisch simulatiemodel ontwikkeld om meer inzicht te krijgen in eetgedrag en onderliggende interne (fysiologische) factoren bij varkens. Dit model simuleert verschillende eetpatronen van individueel gehuisvest, groeiende varkens gebaseerd

op motivatie voor eetgedrag. Het model integreert kennis uit fysiologie en ethologie, en combineert groei met een gedragsmodel. Interactie tussen groei en motivatie leidde tot spontaan optredend eetgedrag, wat het mogelijk maakt om de ontwikkeling en oorzaak van groei- en eetpatronen gedurende de gehele groeiperiode te volgen. Fysiologische factoren, beïnvloed door eigenschappen van varkens en voer, zijn belangrijke interne factoren die een effect hebben op eetgedrag. Modelresultaten bestonden uit eetpatronen op korte termijn (bijv. maaltijdgrootte en maaltijdfrequentie) en groeiparameters (bijv. energieverbruik en lichaamsgewichtstoename). De modelresultaten zijn gevalideerd met empirische gegevens. Dit model verklaart de verandering in eetgedrag en onderliggende motivatie van varkens gedurende de gehele groeiperiode van ongeveer 25 tot 130 kg lichaamsgewicht. Bovendien biedt dit model inzicht in het belang van fysiologische factoren, en varkens- en voereigenschappen die eetmotivatie beïnvloeden.

Varkens laten een 24-uurs “alternans” eetpatroon zien; dat wil zeggen een kleine piek van voeropname aan het begin van de dag en een grotere piek aan het einde van de dag. Om meer inzicht te krijgen in mechanismen die dit eetpatroon veroorzaken, zijn hormonale 24-uurs (circadiane) ritmes in het model toegevoegd. Mechanismen in het model zijn: verwerking van eten in het maagdarmsstelsel, fluctuatie in de energiebalans, circadiane ritmes van melatonine en cortisol, en motivationele besluitvorming. Door interacties tussen deze verschillende processen ontstaan bepaalde eetpatronen over 24 uur (bijv. voeropname, maaltijdfrequentie, eetsnelheid). Deze eetpatronen, evenals patronen voor de onderliggende mechanismen (bijv. energieverbruik), komen overeen met empirische gegevens, wat aanduidt dat het model relevante mechanismen bevat. De circadiane ritmes van cortisol en melatonine verklaarden het alternans eetpatroon in varkens. Daarnaast beïnvloedde de timing en amplitude van cortisolpieken de dag- en nacht pieken in eetgedrag. Modelresultaten laten zien dat de hormonen melatonine en cortisol rechtstreeks het energiemetabolisme kunnen beïnvloeden en daardoor het eetgedrag aansturen, terwijl andere hormonen, zoals leptine en ghreline, het eetgedrag alleen kunnen beïnvloeden in afhankelijkheid van de energiestatus van het dier.

In een volgende stap werd een individu-gebaseerd model van eetgedrag en sociale interactie bij varkens ontwikkeld om eetgedrag van varkens in commerciële huisvesting te simuleren. In dit model werden meerdere varkens en sociale factoren opgenomen om meer inzicht te krijgen in de complexe interactie tussen interne fysiologische factoren en externe sociale factoren. Dieren die in groepen leven, concurreren met elkaar voor voedsel en ondervinden sociale conflicten. Sociale factoren (bijv. competitie en sociale facilitatie) en gedragsstrategieën (bijv. vermijding en benadering) beïnvloeden sociale interacties tussen varkens en hun eetgedrag. Uit de modelresultaten blijkt dat eetpatronen, met name de eettijd, de concurrentie kunnen beïnvloeden en conflicten rondom toegang tot het voer kunnen veroorzaken. Boven een bepaald competitieniveau worden maaltijdpatronen (bijv. maaltijdfrequentie en -grootte) en sociale interactiepatronen (bijv. vermijding en verjagingen) hoofdzakelijk bepaald door gedragsstrategieën. De gemiddelde dagelijkse eettijd per varken kan worden gebruikt om de groeps grootte te voorspellen waarop dit competitieniveau bereikt is. Uit de modelresultaten blijkt dat sociale facilitatie een minder belangrijke rol speelt in de patronen, hoewel het de competitie

tussen varkens kan verhogen. Veranderende eetpatronen, zoals maaltijdfrequentie, eetsnelheid en bezetting van de voerplek gedurende dag en nacht, zijn veelbelovende indicatoren voor dierenwelzijn in varkensproductiesystemen op groepsniveau.

In een volgende studie, is het individu-gebaseerde model van eetgedrag en sociale interactie gebruikt om te begrijpen hoe individuele varkens eigenschappen invloed hebben op variatie in eet-, sociale interactie- en groeipatronen in varkens in groepshuisvesting. Variatie in gedrags- en groeipatronen kan worden verklaard door variatie in varkens eigenschappen die enerzijds fysiologische factoren beïnvloeden en anderzijds gedragsstrategieën bij conflicten. Uit de modelresultaten blijkt dat eigenschappen, zoals groeipotentieel en plek in de dominantieorde, zowel gedrags- en groeipatronen beïnvloeden, alsmede de capaciteiten van varkens om te gaan met sociale beperkingen, zoals bezetting van de voerplaats. Individuele variatie in gedragsstrategieën kan agressie op groepsniveau verminderen, maar kan individuele varkens ook meer vatbaar maken voor sociale beperkingen. Eetpatronen, zoals eetsnelheid of maaltijdfrequentie, zeggen iets anders over dierenwelzijn op groeps- dan op individueel niveau. Een combinatie van eetpatronen, zoals voeropname, eettijd en maaltijdfrequentie, zou geschikt kunnen zijn om varkens met welzijnsrisico's binnen een groep te identificeren.

In dit proefschrift is individu-gebaseerde modellering toegepast om meer inzicht in varkensgedrag en gerelateerde dierenwelzijn en productiviteit te krijgen. Resultaten van het model kunnen welzijnsproblemen aangeven, zoals het aantal conflicten, verjagingen bij de voerplaats, het aantal gewonnen of verloren interacties en niveau van eetmotivatie (honger). Het bevat ook resultaten die de productiviteit kunnen aanduiden, zoals gewichtstoename (met eiwit- en vetafzetting) en de efficiëntie van omzetting van voer naar lichaamsgewicht. Het model kan daarom worden gebruikt om trade-offs en synergiën tussen gedrag en groeiprestatie onder verschillende omstandigheden te analyseren, zoals bij verschillende groepsgrootten en homogene versus heterogene groepen (bijv. met varkens variërend in groeipotentieel, lichaamsgewicht en coping stijl).

Individu-gebaseerd modelleren blijkt een geschikte methode te zijn om diergedrag en onderliggende motivaties te begrijpen. Dit onderzoek heeft bijgedragen aan verder inzicht in eet-, sociaal- en bijtgedrag van varkens in al zijn complexiteit. Ook bleek dat individu-gebaseerd modelleren een nieuwe methode is om gedrag als indicatoren voor dierenwelzijn te vinden en te beoordelen, en om bij te dragen tot het begrijpen van trade-offs en synergiën tussen duurzaamheidsaspecten, zoals dierenwelzijn en productiviteit.



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Iris Boumans,

Volkel, juni 2017







# About the author

Iris Boumans was born on the 12th of August 1981 in Boxmeer, the Netherlands. She obtained her Bachelor degree of Animal Management with a specialisation in Laboratory Animals at van Hall Instituut in Leeuwarden in 2004.



After graduation, she worked part-time in multiple jobs. Six years as course coordinator of the Laboratory Animal Science course for the Academic Medical Center (AMC) in Amsterdam (2004-2010). Two years as research assistant for the animal protection organisation Koningin Sophia Vereeniging tot Bescherming van Dieren, seconded at the Netherlands Centre Alternatives to Animal Use (NCA), Utrecht University (2004-2006). Four years as quality officer for the Animal Research Institute AMC (ARIA) in Amsterdam (2006-2010). And six years as project coordinator for the NCA in Utrecht (2007-2013). Iris won the commission award 'Alternatives for Animal Use' in 2006, which was awarded for her contribution to development of the CD-ROM 'Humane endpoints in laboratory animal experimentation' as a refinement alternative to animal use.

In 2013, she obtained an MSc in Animal Sciences at Wageningen University with a specialisation in Animal Production Systems and Adaptation Physiology. She received the first prize of NZV (Dutch Zootechnical Association) thesis award for her MSc-thesis entitled 'Development strategies of pig farms in the province North Brabant'.

After graduation, she proceeded as PhD student within the Animal Production Systems group of Wageningen University. Her PhD project was part of the IPOP theme 'Complex Adaptive Systems' and IPOP project 'Resilient Pork Production'. Her study focussed on using agent-based modelling for understanding pig behaviour and related sustainability performance in novel farm designs. She received the award for the best oral presentation at the Benelux ISAE (International Society for Applied Ethology) in Sterksel in 2013 and the best oral presentation at the conference Measuring Behavior in Wageningen in 2014. Currently she is employed at the Animal Production Systems group to write a postdoc proposal.



# Publications

## Refereed scientific journals

Hendriksen, C.F.M., Boumans, I.J.M.M. 2013. Learning to be humane. *ATLA* 41, PiLAS 2(2): 16-18.

Boumans, I.J.M.M., Bokkers, E.A.M., Hofstede, G.J., de Boer, I.J.M. 2015. Understanding feeding patterns in growing pigs by modelling growth and motivation. *Applied Animal Behaviour Science* 171: 69-80.

Boumans, I.J.M.M., Hofstede, G.J., Bolhuis, J.E., de Boer, I.J.M., Bokkers, E.A.M. 2016. Agent-based modelling in applied ethology: an exploratory case study of behavioural dynamics in tail biting in pigs. *Applied Animal Behaviour Science* 183: 10-18.

Boumans, I.J.M.M., de Boer, I.J.M., Hofstede, G.J., la Fleur, S.E., Bokkers, E.A.M. 2017. The importance of hormonal circadian rhythms in daily feeding patterns: an illustration with simulated pigs. *Hormones and Behavior* 93: 82-93.

Boumans, I.J.M.M., de Boer, I.J.M., Hofstede, G.J., Bokkers, E.A.M. How social factors and behavioural strategies affect feeding and interaction patterns in pigs in an agent-based model. *Animal Behaviour* (Submitted).

Boumans, I.J.M.M., de Boer, I.J.M., Hofstede, G.J., Bokkers, E.A.M. Unravelling variation in feeding and displacement patterns among pigs using an agent-based model. *Animal Behaviour* (Submitted).

## Abstracts in conference proceedings

Boumans, I.J.M.M., Hofstede, G.J., Bokkers, E.A.M., de Boer, I.J.M. 2013. An agent-based model of tail biting behaviour in pigs. In: Book of Abstracts of the joint meeting of the 33rd International Ethological Conference (IEC) & the Association for the Study of Animals Behaviour (ASAB), August 4 – 8, Newcastle-Gateshead, United Kingdom.

Boumans, I.J.M.M., Hofstede, G.J., Bokkers, E.A.M., de Boer, I.J.M. 2013. Modelling tail biting behaviour in pigs. In: Proceedings of the Benelux ISAE conference 2013, October 10, Sterksel, the Netherlands.

Boumans, I.J.M.M., Hofstede, G.J., de Boer, I.J.M., Bokkers, E.A.M. 2014. Modelling feeding behaviour and associated welfare and productivity of pigs: an agent based approach. In: Proceedings of Measuring Behavior 2014, August 27-29, Wageningen, the Netherlands.

Boumans, I.J.M.M., Bokkers, E.A.M., Hofstede, G.J., de Boer, I.J.M. 2014. Understanding feeding behaviour and associated welfare of pigs from a motivational perspective. In: Proceedings of the 6th International Conference on the Assessment of Animal Welfare at Farm and Group Level, September 3-5, Clermont-Ferrand, France.

Boumans, I.J.M.M., Bokkers, E.A.M., Hofstede, G.J., de Boer, I.J.M. 2015. Modelling causation and development of feeding patterns in growing pigs. In: Book of abstracts of BEHAVIOUR 2015, August 9-14, Cairns, Australia.

Boumans, I.J.M.M., Bokkers, E.A.M., Hofstede, G.J., de Boer, I.J.M. 2016. Explaining daily feeding patterns in pigs: modelling interaction between metabolic processes and circadian rhythm. In: Proceedings of the 50th Congress of the International Society for Applied Ethology. July 12-15, Edinburgh, United Kingdom.

### **Model publications**

Boumans, I.J.M.M. 2016. "Tail biting behaviour in pigs" (Version 4). CoMSES Computational Model Library. Retrieved from:  
<https://www.openabm.org/model/5010/version/4>.

Boumans, I.J.M.M. 2017. "A model on feeding and social interaction behaviour of pigs" (Version 1). CoMSES Computational Model Library. Retrieved from:  
<https://www.openabm.org/model/5628/version/1>.

### **Other publications**

Hendriksen, C.F.M., Boumans, I.J.M.M. 2006. Een rapport over de ontwikkelingen in en rondom het proefdiergebruik en alternatieven voor dierproeven. De proefdierbarometer.

Van Cappellen, J., Boumans, I.J.M.M., Stassen, E.N. 2013. Praktijk weerbarstig bij aanpak kalverdiarree. *Veeteelt* 30 (7). p. 38 - 39.





# Education certificate

Completed training and supervision plan<sup>1</sup>

**The basic package** **3.0 ECTS**

**International conferences** **6.9 ECTS**

BEHAVIOUR, Newcastle, United Kingdom	2013
ISAE Benelux, Sterksel, the Netherlands	2013
Measuring Behavior, Wageningen, the Netherlands	2014
WAFL, Clermont-Ferrand, France	2014
ISAE Benelux, Eersel, the Netherlands	2014
BEHAVIOUR, Cairns, Australia	2015
ISAE, Edinburgh, United Kingdom	2016

**Seminars and workshops** **4.3 ECTS**

ADP seminar 'Aspects of sow and piglet performance', Wageningen, the Netherlands	2013
Masterclass 'Zicht op staartbijten', Sterksel, the Netherlands	2013
NVTB retreat, Schoorl, the Netherlands	2013-2014
Symposium 'Fibres in food and feed', Wageningen, the Netherlands	2013
Wageningen PhD Symposium, Wageningen, the Netherlands	2013
CAS workshop 'Social unrest among humans and animals, Wageningen, the Netherlands	2014
APS symposium 'Solutions for climate change from animal production', Wageningen, the Netherlands	2014
ADP symposium 'Pigs in the picture', Wageningen, the Netherlands	2014
EPOS course 'Connecting minds and sharing emotions in man and animal, Leiden, the Netherlands	2016
WIAS Science day, Wageningen, the Netherlands	2014-2016

<sup>1</sup> With the educational activities listed, the PhD candidate has complied with the educational requirements set by the graduate school Wageningen Institute of Animal Sciences (WIAS) of Wageningen University & Research, which comprises a minimum of 30 ECTS (European Credit Transfer and accumulation System). One ECTS equals a study load of 28 hours.

<b><u>Presentations</u></b>	<b><u>12.0 ECTS</u></b>
Theatre, BEHAVIOUR, Newcastle, United Kingdom	2013
Theatre, ISAE Benelux, Sterksel, the Netherlands	2013
Theatre, Wageningen PhD Symposium, Wageningen, the Netherlands	2013
Theatre, CAS Workshop, Wageningen, the Netherlands	2014
Poster, WIAS Science day, Wageningen, the Netherlands	2014
Theatre, NVTB retreat, Schoorl, the Netherlands	2014
Theatre, Measuring Behavior, Wageningen, the Netherlands	2014
Theatre, WAFL, Clermont-Ferrand, France	2014
Poster, WIAS Science day, Wageningen, the Netherlands	2015
Theatre, WASS lecture, Wageningen, the Netherlands	2015
Theatre, BEHAVIOUR, Cairns, Australia	2015
Theatre, ISAE, Edinburgh, United Kingdom	2016
<b><u>In-depth courses</u></b>	<b><u>10.0 ECTS</u></b>
Course simulating emergence, Wageningen, the Netherlands	2013
Summerschool individual- and agent-based modelling, Dresden, Germany	2015
<b><u>Professional skills support courses</u></b>	<b><u>3.0 ECTS</u></b>
Reviewing a scientific paper, Wageningen, the Netherlands	2013
Techniques for writing and presenting a scientific paper, Wageningen, the Netherlands	2014
Course supervising MSC thesis work, Wageningen, the Netherlands	2014
Orientation on teaching for PhD candidates, Wageningen, the Netherlands	2015
<b><u>Didactic skills training</u></b>	<b><u>15.0 ECTS</u></b>
Coordinating and lecturing GSAP21	2014
Supervision of 3 BSc theses	2014-2016
Supervision of 5 MSc theses	2013-2016
<b><u>Education and training total</u></b>	<b><u>54.0 ECTS</u></b>





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