

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



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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.

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1. Introduction

Current intensive pig production systems are subject to major sustainability concerns, including concerns about pig welfare (Krystallis et al., 2009; Averós et al., 2010). 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 and 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 m² per animal or less (EFSA, 2007b). These housing conditions can lead to several welfare issues, such as tail biting and leg injuries (EFSA, 2007a; Averós et al., 2010). 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 and 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,

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the use of this method in applied ethology and animal welfare science has been limited so far (Asher et al., 2009; Collins and 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 (Schröder-Petersen and Simonsen, 2001; D'Eath et al., 2014). 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 (Schröder-Petersen and Simonsen, 2001; D'Eath et al., 2014).

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. 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 et al., 2005; Grimm and Railsback, 2012). 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 and Railsback, 2012). It would then count as an explanation of the causation of these patterns.

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. 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.

2.2.1. 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 (Schröder-Petersen and 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 (Schröder-Petersen and 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. 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 and 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.

2.2.3. 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).

2.3. 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?

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.,

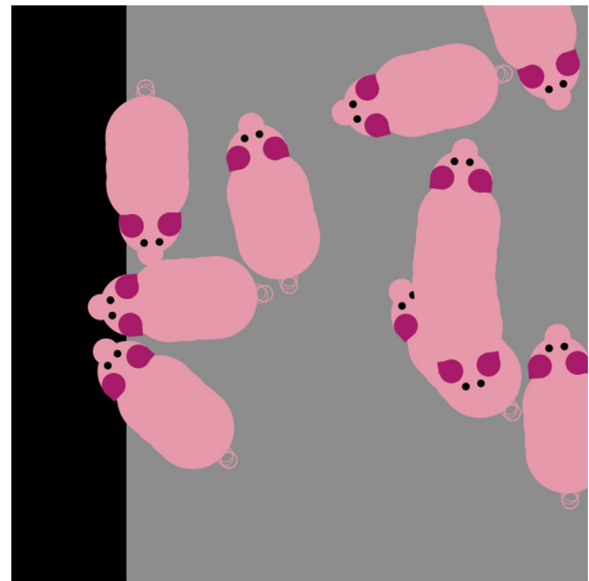


Fig. 1. Graphical interface of the model. The model represents a barren pen with concrete floor (grey), feeding space (black) and ten pigs.

2010) are available in the model library of the OpenABM website (<http://www.openabm.org>).

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 (Fig. 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.

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., 2005). 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. (2005). 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).

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 (Fig. 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

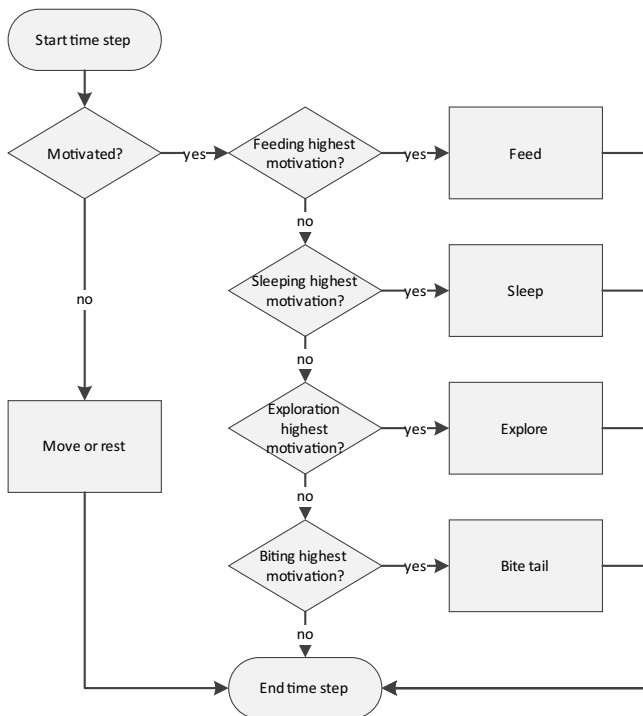


Fig. 2. Flowchart of the processes for performing a behaviour in the model for one pig each time step.

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., 2005).

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.

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 min) in which pigs are more active. Tail biting behaviour seems to occur especially in this period (Schröder-Petersen and Simonsen, 2001).

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.

5. Model results

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%–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 (Fig. 3). Pigs that were tail biting (18.4% of the pigs) spent on average 0.15% of their time on tail biting behaviour (Fig. 4).

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%–0.24%) and 0.07% (range 0%–0.26%), respectively. To illustrate the variation in patterns between simulations, a run with a low level of tail biting behaviour (Fig. 5a) and a run with a high level of tail biting behaviour (Fig. 5b) is displayed. CHANGE decreased the number of neutral pigs and increased the number of pigs that were both biter and victim (Fig. 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 (Fig. 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 (Fig. 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.

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
Performing pig						
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 ^b	-	-0.09
Receiving pig						
Biting drive	-	-	-	-	-	0.05 ^a
Sleeping drive	-	-	-	-	-	-0.20 ^a

^a If impact of tail biting on a victim was included in the simulation.

^b 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).

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^a.

Parameter	Reference value	Parameter alteration (%)	Tail biting behaviour (%)	Neutral (%)	Biter (%)	Victim (%)	Biter & victim (%)
<i>Scenario 1^b</i>			0.03	67.3	14.6	14.3	3.8
<i>Effect of number of pigs and duration^c</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^c</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 biting threshold	0.05	-50	0.02	69.4	14.4	14	2.2
		+50	0.03	64.1	15.5	16.9	3.5
<i>Scenario 4^b</i>			0.07	52.1	9.1	7.9	30.9
<i>Effect of tail biting behaviour on victim^d</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

^a Values are averages of 100 simulations.

^b Results of the model with initial parameter values.

^c Tested in scenario 1 (with motivation to bite as only factor included).

^d Tested in scenario 4 (all factors included).

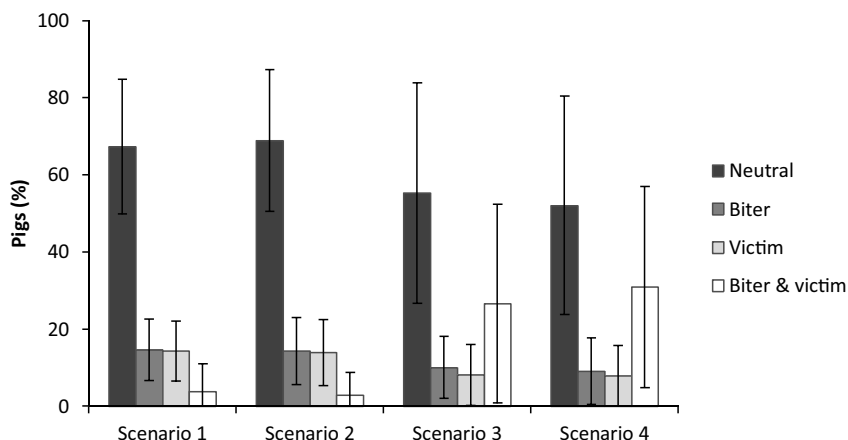


Fig. 3. The average and standard deviation of distribution of pigs into tail biting categories (neutral, biter, victim or biter and victim) in four scenarios. Simulations of each scenario were repeated 100 times.

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%–0.07%) was

similar to scenario 1 (0.03%, within a range of 0%–0.08%). And the average tail biting behaviour in scenario 4 (0.07%, within a range of 0%–0.26%) was similar to scenario 3 (0.06%, within a range of 0%–0.24%). Adding PREFERENCE slightly increased the number of

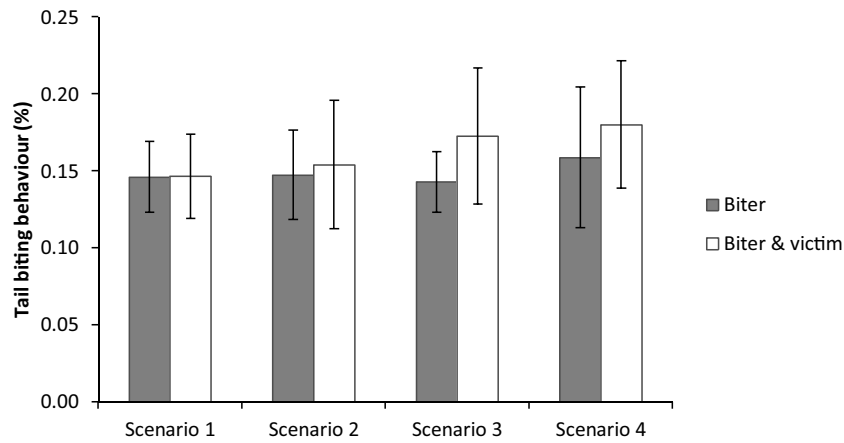


Fig. 4. The average and standard deviation of time spent on tail biting behaviour of pigs that are biter or biter and victim in four scenarios. Simulations of each scenario were repeated 100 times.

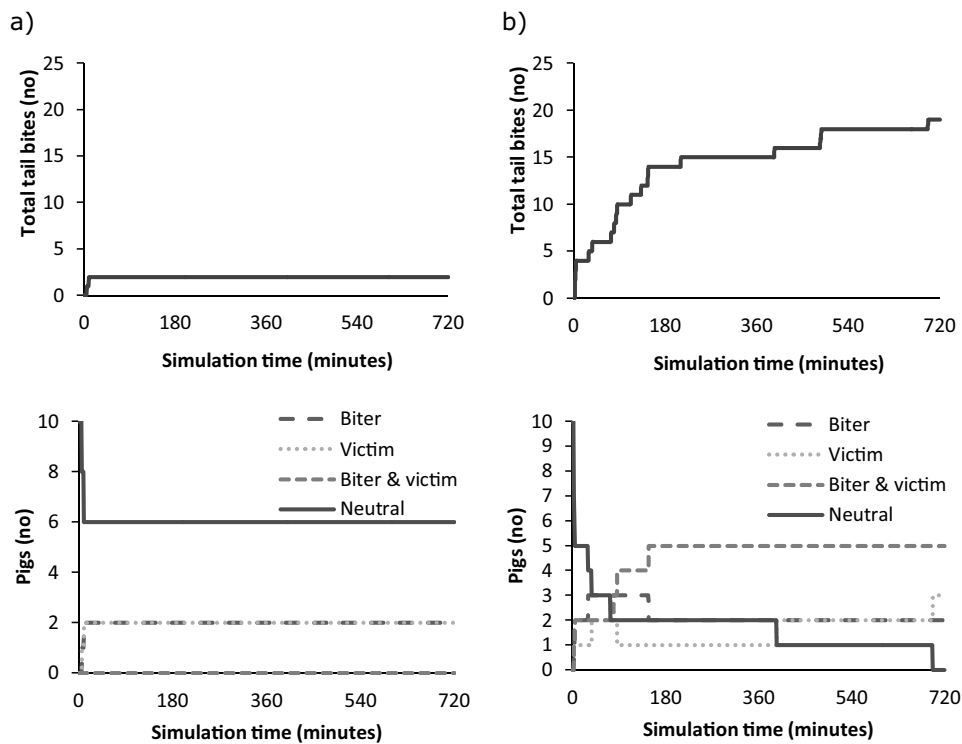


Fig. 5. Development of tail biting incidents and categorisation of pigs in model scenario 4 during a run with a) 2 biting incidents (0.03% tail biting) and b) 19 biting incidents (0.26% tail biting).

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%) (Fig. 3).

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%–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.

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.

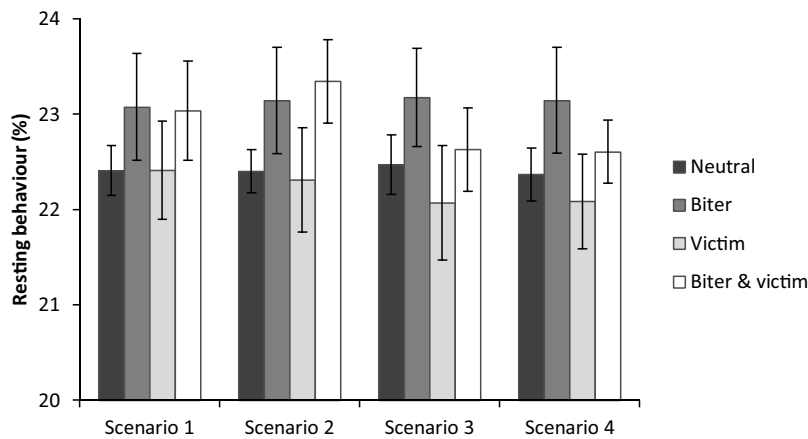


Fig. 6. The average and standard deviation of time spent on resting behaviour of pigs in the four tail biting categories (neutral, biter, victim or biter and victim) in four scenarios. Simulations of each scenario were repeated 100 times.

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., 2005). 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 effect. 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 3–5% (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.

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 and Sumpter, 2007; Collins et al., 2011). Understanding how a behaviour is caused can require considerable detail in processes (Tichit et al., 2009; Boumans et al., 2015). 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.

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.

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