12-2-2018

Towards a common conceptual framework and illustrative model for feather pecking in poultry and tail biting in pigs – Connecting science to solutions

Marc B.M. Bracke[a], T. Bas Rodenburg[b], Herman M. Vermeer[a], Thea G.C.M. van Niekerk[a]
[a] Wageningen Livestock Research
[b] Wageningen University, Dept. of behavioural ecology
Corresponding author: marc.bracke@wur.nl

Reading guide

This is one of 8 blog posts under the heading of: "**Towards a common conceptual framework and illustrative model for feather pecking in poultry and tail biting in pigs – Connecting science to solutions**". It contains the following sections/posts:

1. Introduction

Feather pecking (fp) in poultry and tail biting (tb) in pigs are among the most persistent animal-welfare problems associated with intensive livestock farming. Both problems have been studied and reviewed extensively (e.g. fp: (Rodenburg et al., 2008; Nicol et al., 2013; Rodenburg et al., 2013); tb: (Schrøder-Petersen and Simonsen, 2001; Bracke et al., 2004a; EFSA, 2007b; Taylor et al., 2010; D'Eath et al., 2014; Valros, 2017)). Legislation and policy initiatives have been discouraging the continued performance of routine mutilations (beak treatment and tail docking for fp and tb respectively). However, both poultry and pig farmers generally find it difficult to stop mutilations and prevent and/or treat these injurious behaviours in intensive farming systems. Comparing fp and tb may help address these problems. However, few papers have compared the two forms of abnormal behaviour in detail. One notable exception is the fairly recent Open-Access publication by Brunberg et al. (2016). These authors discussed similarities and differences between fp and tb, and presented a general model which looks somewhat like an envelope. This publication is written for a scientific audience, and it is not easy to read for farmers and others interested in solving fp/tb such as vets, other farm advisors and NGOs. Also the 'envelope-shaped' model presented by Brunberg et al. (2016) is not as appealing as we would (ideally) like it to be. It mainly says that by nature both pigs and poultry are omnivorous generalists that have (had to) become production specialists via genetic selection and rearing in large-scale intensive systems applying a one-size-fits-all principle. According to Brunberg et al. both the physical and social environment ('where you are' and 'who is with you'), together with animal-related factors ('who you are') determines 'what you become' in terms of fp or tb, i.e. a performer (pecker/biter), victim/receiver or a neutral animal. The authors also hypothesise that the gut-microbiota-brain axis may play a crucial role which should be investigated further. This is in accordance with the common view that fp and tb are multifactorial problems associated with the substantial discrepancy between the natural and the commercial environment resulting in a (seriously) deprived foraging (and/or feeding) motivation that eventually leads to fp/tb (and worse, i.e. cannibalism, if not curtailed adequately).

It is not entirely clear, however, why the model (figure) in Brunberg et al. (2016) should look like an envelope. When looking a bit more closely at the figure, the model appears to encompass everything (the animal, its history and its entire, physical and social, environment). Only upon more careful examination and in particular when reading the text itself do the further ramifications underlying the model become more clear. Since we feel the text may be rather inaccessible for practical application in problem solving, one objective of these blog posts, therefore, is to compare this model to other models, esp. those developed in our own organisation (Wageningen University & Research), in order to see if we can better highlight the available knowledge that should be used to (eventually help) solve the problem in practice. To this end we have also tried to make the information presented by Brunberg et al. (2016) more accessible, and we supplemented it with our personal expertise on fp/tb. It is important to emphasise, however, that the primary aim of this publication is to improve on the available conceptual frameworks to facilitate practical understanding of fp and tb so as to support solving the problem in the future. We do not, however, aim to present a tool box or cook book for solving fp/tb.

2. Terminology

In the next posts we will summarise similarities and differences between feather pecking (fp) in laying hens and tail biting (tb) in pigs, taking Brunberg et al (2016) as a starting point. We will also characterise the different models that have been proposed before on fp/tb. Building on this we will argue why we think that fp/tb may/should be regarded as a medical/mental disorder, provided the medical framework maintains an evolutionary and scientific perspective on fp/tb.
This post aims to characterise the underlying concepts and criteria, so as to illustrate that giving crisp definitions may not be as easy as it may seem to be at first sight.
Semantically, *feather pecking* (fp) and *tail biting* (tb) are terms that refer to a behaviour, respectively pecking at feathers and biting a tail. However, in practice the terms are also frequently used not to refer to the behaviour (which is not always easy to observe), but to the clinical consequences, namely the presence of wounds due to fp/tb. Both fp and tb is penmate-directed behaviour (hence fp differs from feather pulling observed in e.g. parrots (van Zeeland et al., 2009), which is self-directed behaviour). Both fp and tb are mutilating behaviours, i.e. they may (but do not have to) result in wounds. Thus, both fp and tb tend to be labelled as 'severe' when resulting in wounds, while the less severe forms of the behaviour are labelled 'gentle fp' and 'tail-in-mouth' (TIM) respectively. Note that when the terms are used to refer to clinically observable wounds, the terms (fp and tb) may be regarded as proxies for severe fp/tb (but not the gentle forms). The phrase TIM also indicates a problem in science, namely that the actual biting/pecking behaviour itself is not always easily observed (e.g. on video recordings). Like using the label 'feeding' when in fact 'nose in feeder' behaviour is observed, fp/tb may be used as a proxy, e.g. 'nose near tail' (with/without a response in the receiver) in the case of pigs. In addition, not all scientists and farmers use the same definition of what they (would) label as fp/tb behaviour and/or as a fp/tb wound. For example, it may depend on the time available to do the observation, the distance to the pigs, pen soiling and the lighting conditions under which the observations take place. Thus, what appears to be clear-cut terms, may not always refer to the same observed phenomena as ideally needed to facilitate the interpretation of the results of scientific studies for practical application. This semantic differentiation of fp/tb also points towards the notion that (the concepts of) fp/tb are not fully independent of the observer.
Note: We will use the label 'fp/tb' in the remainder of these related posts to refer to the communal problem. It is difficult to provide an *overarching term* for fp and tb together. Most existing terms are too wide: Abnormal behaviour, injurious behaviour and harmful-social behaviour, e.g. because there are other forms of abnormal behaviour and because there are other forms of injurious behaviours like aggression (e.g. vulva-biting in sows) and abrasive behaviours (injuries resulting from making contact to flooring or pen fittings; cf fin injuries in farmed fish (Noble et al., 2012; Stien et al., 2013; Pettersen et al., 2014; Folkedal et al., 2016)).
An *outbreak* of injurious fp/tb requires a specification of the start and end point, i.c. presence of injuries. Here, again, the observer may play a significant role: the detection of injuries depends e.g. on the inspection frequency and quality (e.g. method & expertise) of the observer. The observer also plays a role in so-called early-detection and in decision-making as to when and what *treatment* is to be started to counteract an on-going outbreak.

It should also be emphasized that fp/tb is a *process*, where different types of animals are involved. In order to start, one '*neutral*' animal must become an *actor* (pecker/biter) showing fp/tb behaviour towards a *victim*/receiver resulting in a fp/tb wound. When the outbreak escalates more and more individuals become involved and/or wounds become progressively severe, potentially leading to the death of the victim (such that the fp/tb may at some point be called '*cannibalism*'). Wounds may also get infected, thereby aggravating the impact on productivity and welfare. Some animals in a fp/tb pen may not get involved. These may be labelled 'neutrals'. In addition, Brunberg et al. (2016) use the term '*controls*' for animals in neighbouring pens which are not affected by fp/tb. These different types of individuals involves are not fixed over time. E.g. both neutrals and controls are labels that may changes over time (Daigle et al., 2015), i.e. animals that were neutrals/controls today, may become actors or victims tomorrow, and individuals may be both actor and victim at some point in time (or even at the same time). When an outbreak ends, both actors and victims may return to being 'neutrals', even though it is generally recognised that the probability of recurrence is much bigger in groups that have previously experienced fp/tb problems, as if the 'set points' of such animals have changed irreversibly. Because of this rather irreversible state-change it is important to differentiate between *prevention*, what is done to prevent an outbreak, and curative *treatment*, what is done to stop an outbreak that has occurred.
A final term used in these posts is the word *'model'*, by which we primarily mean a figure intended to explain fp/tb. Ideally, the model should not only illustrate the mechanism and the types of individuals involved, and where/how it goes wrong (e.g. that fp/tb is a multifactorial problem), but also provide answers to the other 3 why questions (evolution, function, ontogeny). Ideally, also the model should explain anomalies (i.e. apparently 'strange' facts) and generate testable predictions. The ideal model should also be effective in communicating what is the (e.g. welfare or production) problem associated with fp/tb and provide suggestions regarding prevention and/or treatment. Also, a model is better if it uses a stronger, more intuitively appealing metaphor, such that it is easily remembered, not only by scientists, but also by other stakeholders, i.e. farmers, their advisors, and NGOs (see e.g. cartoons at http://www.featherwel.org/). However, besides addressing all of these aspects, a good model should not be complex, but rather explain fp/tb in the most parsimonious way possible.

3. Overview of main similarities and differences between feather pecking and tail biting

Table 1 shows an overview of similarities and differences between feather pecking (fp) in poultry (i.c. laying hens) and tail biting (tb) in pigs (i.c. weaned and growing/fattening pigs).
Table 1 is based primarily on Brunberg et al. (2016) and supplemented with our own (esp. MB and TvN) knowledge about fp and tb (also as presented on the henhub website www.henhub.eu). The table is intended to summarise the most relevant similarities and differences between fp (in hens) and tb (in pigs), and thus support decision making in dealing with fp/tb in practice.
The key risk in fp/tb is the fact that both laying hens and pigs are originally omnivorous generalists that have been become production specialists in feed intake and food conversion in intensive farming conditions. The motivation for fp/tb relates to a frustrated foraging need, which is modulated by a whole array of different risk factors, hence resulting in this multifactorial welfare issue. In addition to similarities the table also identifies a number of differences between fp in layers and tb in pigs, e.g. we don't have genetically selected lines for tail biting comparable to the high and low fp lines in poultry. Hence, an experimental model to study tb in more detail is currently largely lacking (though pigs selected for social breeding value (high indirect genetic effects for growth) showed considerably less ear biting, tail damage, aggression and enrichment manipulation (Camerlink et al., 2015), and may thus in principle be suited to be used to study tb experimentally in more detail).
The table may perhaps be improved upon further by specifying relationships between the items specified as risk factors (in the left column) and the different responses identified in the process of fp/tb (in the right column; cf (Fraser, 1987a)).
Another suggestion relates to the many risk factors that may hamper practical problem solving. While scientific experiments necessarily vary only a few risk factors in order to reliably examine which factors may affect fp/tb, a tentative suggestion for solving the multifactorial fp/tb problem could be to try to

formulate multifactorial solutions. This may be esp. relevant when monofactorial solutions fail to solve the problem. However, an important drawback of this approach is that it may essentially remain unclear which factors are accountable for any (positive or negative) results. When a multifactorial approach is working, it may be possible to tease out in subsequent research the relative contribution of the different risk factors. When it doesn't work, that may be the end of the road for that particular type of farming (given the constraints imposed).

1

Table 1. Comparing risk factors and animal responses related to feather pecking (fp) in poultry (laying hens) and tail biting (tb) in pigs, taking Brunberg et al. (2016) as a starting point, supplemented with own author expertise (marked as *). Common risk factors (similar across species, specified between brackets when 'unknown') are followed by notable differences between Hens and Pigs (specified on the next lines). Black characters: risk increasing factors; green: risk decreasing factors (benefits); red (in the column 'risk factors'): particularly welfare-reducing risk factors. 'No': means that the opposite reduced fp/tb.; behav.: behaviour; envir.: environment; decr.: decreased; incr.: increased; HFP: high fp line/breed; LFP: low fp line; TIM: tail-in-mouth; w: weeks; d: days; mo: months. The cells in column 'Responses' are not directly (horizontally) related to the risk factors. Responses are stacked: more positive behaviours are presented at the bottom; worst (form of escalation, i.e. cannibalism) is shown on top. Responses are related to 'type of animal' (victim, actor, neutral) (with welfare aspects specified at the level of the type-of-animal label). Poor welfare responses are shown in red (in the column 'responses'). See the text for a more detailed description of how to read the table.

Type of factor	**Risk factors (Multifactorial, related to the type of factor, i.e. environment-, group- & animal based)**	**Responses (behav., physiology, pathology & welfare, related to type of animal, i.e. victim, actor, neutral)**	**Type of animal**
Envir.-based	Modern large-scale specialised farms	Victim: fear, pain (during outbreak), stress, sickness (during treatment, recovery)	Victim
	Barren pen (no proper foraging material, straw), large discrepancy between intensive farming envir. and the natural envir./envir. of evolutionary adaptation	Cannibalism	
	(Partly) slatted floor Hens: (Litter) Pigs: Concrete	(Wound) infection	
	Indoors* Hens: Range (may provide foraging opportunities and reduce stocking density) Pigs: - (Outdoor area may provide rooting substrate (soil), fibre (pasture), but not necessarily) One size fits all (food, climate*)	Production loss (reduced growth) Hens: Egg laying (reproduction) Pigs: Growth (production)	
	Standardised feed, optimised for average individual (vs indiv. needs); perhaps probiotics may treat fp/tb Hens: - Pigs: No phase feeding; decr. feeding frequency predicted tb outbreaks 9 w later; tb victims made more feeder visits 2-5w prior to tb	Appearance Hens: Deteriorating feather cover Pigs: Tucked tails	

	Feed changes and 'hiccups' in providing feed (unpredictable frustration) Feed type; Reduced feeding time, not ground, concentrated feed, less fibre Hens: Pellets give more fp than fine ground feed; no mash/pecking materials; high E diet; no feathers in diet (acting as fibre, incr. feed passage) Pigs: Contradictory results (liquid/pellets/meal) but straw reduces tb & is consumed Protein, mineral (NaCl) deficiency; supra-nutritional NaCl may alleviate fp/tb Hens: Deficiency of crude protein, amino acids, minerals (Na, Ca) Pigs: Nutritional imbalance incr. tb	Decreased tryptophan, serotonin levels (Fp/tb) Wound(s) Hens: Esp. tail, body (not back of head) Pigs: Tail (possibly ears, flanks, legs)
	Feeder space, feed competition (bite/peck to get access to feed) Rearing conditions (both poor rearing conditions and a backdrop from enriched rearing conditions to deprived conditions later in life) Hens: Absence of litter around 5w, high stocking densities, rearing on wire floor Pigs: More piglets/stockperson, fostering, no straw in farrowing pen, reduced feeder space during rearing gives more tb later in life; multi-litter rearing decr. manipulative behav.; providing straw during rearing and then depriving pigs of straw later is also considered a risk factor	Salivation (pH incr.; alleviate peptic ulcers) [Microbiota composition?] Hens: HFP has different microbiota composition than LFP; feather eating changes gut microbiota; Pigs: Unknown
	(Pen size, pen design) Hens: (Large) Pigs: (Small)	Escalation of tp/tb (outbreak)
Group-based (envir.- & animal based)	Group housing Hens: (Very) large groups (10-100.000 birds) Pigs: Small (~10 pigs) High stocking density Hens: More fp in largest groups (15-120 birds) Pigs: (Not uniform results) Farm health status (any (major) stressor/immune suppressor probably) Hens: Vaccination (specific immune stimulation) when young may incr. fp as adults; LFP have better immunocompetence; e.g. E. Coli incr. severe fp Pigs: Better health status reduces tb; straw reduces infections	Arousal, restlessness, excitement (positive), fear & avoidance (negative). Hens: Cut feathers increased fp Pigs: Blood tail model (rope) increased (tail) biting behav. Cognition, (social) learning, (synchronisation; copy-behaviour; stimulus enhancement) Prevalence/intensity: Hens: Fp on 86% of UK flocks; SFP esp. when adult; fp up to 135 bouts/bird/hr; 3 severe pecks/min Pigs: Tb on 30-70% of farms; fanatic biters bite 11-25% of time

	Mutilation (3 aspects are relevant: 1. Method used; 2. Amount of tissue removed; 3. Age of treatment; esp. 2nd aspects is relevant as risk factor) Hens: Beak treatment (previous beak trimming (may remove larger/smaller part of the beak), now infrared beak treatment) (Note: In poultry, as it were the (future) actor is mutilated) Pigs: Tail docking (longer or shorter part of the tail) (Note: in pigs as it were the (future) receiver is mutilated by removing the tail)	Severe fp (SFP)/tb Hens: - Pigs: Three types of (severe/injurious) tb: two-stage (starting with TIM), sudden forceful, and obsessive (fanatic)	
	History of fp/tb (once an outbreak has occurred, the likelihood of another outbreak increases; animals are never the same again after an outbreak; (irreversibly) changed set points)	Actor: (Excitement, pleasure [during outbreak], pain, stress [during treatment]) Hens: Pecker Pigs: Biter Object-direction: Hens: Towards feathers Pigs: Towards the tail	Actor, performer
Animal-based	(Bred for) very high production-efficiency (genetics, breeds) (esp. genetic motivation of feed-related behav.; behavioural need to species-specific foraging behav); fp/tb has moderate heritability (~0.2) Hens: (Eggs) Pigs: Lean meat; neutrals have different genetics Domesticated 5-6000 years ago; bred in 50 years of intensive selection from foraging generalists (omnivorous (variable diet; need to explore)) to meat & egg producing specialists; fp/tb not selected against; tb&fp are correlated to production, but not in the same way Hens: Male peckers had higher body fat; female peckers had earlier onset of lay; HFP: Better growth, lower total egg mass, decr. feed efficiency Pigs: Lower backfat, lean tissue growth Being different Hens: Plumage colour (standing out from others; incidental pigmented birds were more often victims) Pigs: [Lame pigs get bitten]	Neutral (in same pen)/control (on other pen): Neutral as a biter in spe: boredom, frustration, behavioural deprivation, esp. of foraging motivation Gentle manipulation Hens: Gentle fp is prevalent in young birds, decr. with age Pigs: Tail in mouth (TIM), Pen-mate directed exploration Hens: (Deteriorated) plumage condition Pigs: Wet tails Consummatory behav.: Hens: Feather eating (more in HFP) Pigs: - Object/substrate-directed exploration/foraging in accordance with nature, showing natural behav. (50-60% of time) Hens: Scratching, pecking Pigs: Rooting, biting	Neutral / control

	Personality Hens: Peckers appear more proactive, fearful (in open field), stress (cortisol shows variable results); more foraging & walking when young incr. fp as adults; HFP more active; mobility to get to the nestboxes (i.e. too calm birds are at risk for fp) Pigs: Low backtest responders showed less pen-mate manipulation; biters more sitting & kneeling 6d prior to tb; victims more posture changes 6 d prior to tb; tail posture (tucked) may predict tb 2-3d before outbreak		
	Sex, probably females more active performers Hens: All females Pigs: Mixed/uni-sex; males receive more tb; uncastrated males are more likely to become fanatic biters (1 study)		
	Age: Onset around sexual maturity (also then shifting nutritional needs) Hens: Adult (16-80wks); progesterone (& oestrogen) incr. up to 18w incr. fp; testosterone decr. fp; SFP ~20w in females, but not males Pigs: Young, prepubertal (<5-6mo); perhaps associated with teething*		
	Body weight Hens: - Pigs: Biters are lighter; victims tend to be heavier before tb (later decr. growth)		

4. Farmer as a risk factor

Though not specified in Brunberg et al. (2016) human stakeholders, i.c. the farmer, may also be included in the description of feather pecking (fp)/tail biting (tb). Since the farmer must make management decisions (at many different levels), he/she will affect all other risk factors involved in fp/tb. In fact, it has been proposed that the farmer may be the most important risk factor (Van Dooren, 2013; Zonderland and Zonderland-Thomassen, 2016). Like the animals, farmers will be showing behavioural responses, and farmers may also experience welfare problems in case of fp/tb.

As is the case for the animal, what matters to the farmer is how (s)he perceives the problem (rather than what is the problem in 'reality' (Uexküll, 1909)). For example, laying hens living in a multilayer system (volière) may be perceived as having access to litter. However, what matters to welfare is how the animal perceives its environment, e.g. a hen living in the upper tiers may not have access to litter, thus live in an environment without litter (and thus be more prone to fp). Similarly, a farmer who believes that beak treatment/tail docking is painless (a false belief), or who has a strong aversion to pecking/biting wounds may not have the motivation required to (try to) end the practice of routine preventive mutilations. Thus what matters is how the problem is perceived. The farmer's problem solving in case of fp/tb may be hampered by being 'allergic' (e.g. to wounded animals due) to fp/tb, and by being 'lethargic' (e.g. being unable to respond adequately when active treatment is called for when fp/tb starts). While the farmer has the end responsibility of how his animals are reared, other stakeholders also play a role, e.g. a farmer's ability to deal with fp/tb may depend on other farmers (e.g. who are rearing his animals, or who ventilate opinions as to whether ending mutilations is (not) desirable), the market (e.g. the retailer who is buying his eggs/pigs), the government (issuing legislation and taking policy measures to simulate and/or discourage certain practices), and farm advisors (e.g. providing/withholding knowledge and support required to deal with the fp/tb problem). Table 2 lists main farmer-related risk factors and responses involved in fp/tb. Note: we have decided to incorporate the responses in the list of risk factors, because the way a farmer responds to fp/tb (prevention, treatment, early-detection) is itself part of the farm management.

Table 2. Farmer-related risk factors of feather pecking (fp) and tail biting (tb), and farmer-related responses related to the type of factor (environment-based; farmer-based, and response-based (1; curative treatment; 2: prevention; 3. early detection). Red: welfare reducing aspects.

Farmer-related risk factors (management) & responses (prevention & treatment)	**Type of factor**
Economy, market	Environment-based
Legislation (and its enforcement), policies Social support/pressure, sector/chain image	
Fp/tb specific farm management regarding (timely/delayed) **treatment**: e.g. providing enrichment, identifying & resolving cause(s)/risk factor(s), isolation/removing actor and/or victim, dimming the lights (impaired vision), repellents, mutilation (as a treatment in untreated animals), monitoring (i.e. treatment evaluation). Pigs: teeth cutting (cf beak treatment in Hens: removing animal's 'equipment' to do harm). Hens: spectacles (another form of impaired vision used in the past (before beak trimming was invented, to prevent accurate sight of feathers); culling of peckers (peckers may be identified by their pecking behaviour or perhaps by their relatively unaffected feather cover).	Response [1]
Fp/tb specific farm management regarding **prevention**: e.g. mutilation, enrichment, climate, food, health care, monitoring (early detection)	Response [2]
Fp/tb specific farm management regarding **early detection**: Hens: Reducing feather cover may indicate fp is starting Pigs: Tucked tails, wet tails (possibly reduced feeder visits; enhanced interest in enrichment materials)	Response [3]
General farm management (quality; quantity)	Farmer-based
Knowledge, education Personality (reactive, proactive) Attitudes (towards animal welfare, etc.).	

5. Models

Table 3 shows a list of various models/figures that have been proposed to clarify feather pecking (fp)/tail biting (tb), including the recent model proposed by Brunberg et al. (2016). Our focus here was to compare models, esp. models originating from Wageningen University Research, in search for potential improvements. Not all models have been included in Table 3. For example, Valros and Heinonen (2015) propose a modified bucket model where the bucket is filled with acute and/or chronic stressors (cf also Valros (2017)).

Table 3. Overview of models related to feather pecking/tail biting (fp/tb). gb: general behaviour; ab: abnormal behaviour; aw: animal welfare; behav.: behaviour; obj.: object; incr.: increased.

Author (& ref)	**Ab out**	**Model**	**Metaphor**	**Brief description**	**Main strength(s)**	**Main weakness(es)**
Von Uexküll (1909)	Gb	Homeos tatic	Thermostat	Istwert-Sollwert model where Istwert is the environment as perceived by the organism (Umwelt). Sollwert is norm as determined by evolution.	Emphasises that Istwert is the envir. as perceived by the individual (not as it 'really' is).	Does not explain specific traits of fp/tb (but not specifically designed for fp/tb either).
Lorenz; (1950; 1978)	Gb	Psychoh ydraulic	Water flowing from a reservoir	The motivation to perform a behav. builds up with time and can be reduced only by performance itself; releasing stimuli can make the water flow more easily (unplug reservoir). Water pressure = motivation; water flow = behav.	Shows behav. is process in time (water flow); explains refractory period after behav. has been performed (reluctance to repeat the behav.).	No innate build-up of motivation in the brain; no feedback from behav. (behav. is not goal directed/not affecting the input tap flow in the model); no refractory period for fp/tb; output levels suggest always behav. 1, then always behav. 1 & 2, then always behav 1, 2 & 3, which is not valid.
Wiepke ma (1987)	Aw	Homeos tatic	Thermostat	Animals have evolved cognitive-emotional control mechanisms to deal with a variable environment. Behav. Is motivated by a mismatch between Istwert (actual state) and Sollwert (set point) and is switched off once the Istwert has been changed (via neg. feedback through receptor & evaluation system).	Explains (neg.) welfare (esp. stress) and the role of evolution.	Only about poor welfare (stress); no feed forward loop.
Fraser (1987a)	Tb	Flowcha rt	‘Table’	Column of management factors (e.g. lack of chewable objects; nutrient deficiencies) related to column of behavioural phenomena (e.g. penmate-directed behaviour; attraction to blood).	Tabulates & relates both management and behaviour; differentiates between known and hypothesised relationships.	Two columns and arrows are not intuitively appealing (not a ‘catchy’ model);
Hughes and Duncan (1988)	Ab	Feed forward	Thermostat	Distinguish appetitive and consummatory phases of behaviour and emphasise the presence of a positive feedback from the former to behaviour.	Feed forward (positive feedback may reinforce a behav.).	General model for behav., not specific for fp/tb.

Korte et al. (2007)	Aw	Allostasis	Tilting shed	Long-term exposure to (maladaptive consequences of) 'stress' may represent a risk by its wear and tear effects (so called ''allostatic load''), e.g. persistent exposure to strong winds may make a shed stand tilted (at risk of tipping over when 'challenged').	Emphasises that set points can change (plasticity). Capacity to adapt to changes determines welfare. A narrowed regulatory range (hence incr. chance of hypo-/hyperstimulation) poses a risk.	Not clear what is the added value of this model in relation to fp/tb (model seems comparable to tipping bucket model, see below).
Bracke (2008)	Tb	RICHPIG	Thermostat	Multiple (neg.) feedback loops indicate incr. deviation between norm (need) and actual state.	Detailed model, suitable to build a decision support system (semantic model); includes neg. and pos. welfare; shows relationship between welfare design & performance, and role(s) of present & past (evolutionary & life history).	Complex figure (not appealing); only one animal is shown (which is esp. the actor, but may also be a neutral animal, or victim).
Zonderl and (2010a)	Tb	Diagram	Venn diagram & flow chart	Aetiology model with exploration motivation leading to tb in a group of pigs (biters and victims).	Differentiates biters and victims.	Multifactorial nature and irreversible state change not clearly illustrated.
Zonderl and (2010b)	Tb	Overflowing bucket	Overflowing bucket	Risk factors 'fill' a bucket, tb occurs when the bucket overflows.	Tb results from the accumulation of many risk factors (multifactorial), up to the point of 'escalation'.	Doesn't emphasise state change after onset of tb (same 'titration' as before tb started); normal behav. not shown.
Vermeer (Bracke et al., 2012)	Tb	Tipping a tilted bucket	Tipping bucket	Risk factors 'fill' a tilted bucket, such that the bucket tips over (i.e. falls, when tb occurs).	Shows that tb has the tendency to escalate (small change, big consequence) and that it results in a state change (other, irreversible set point).	State change is too dramatic (bucket cannot get back up, and if so, the model doesn't show state change any more).
Vermeer (Bracke et al., 2012)	Tb	Marble run	Marble run	Some kind of (risk factor) 'force' may push a marble over the (first) hill resulting in an irreversible state change (lower level).	Tb results in a new state of equilibrium, which may be repeated (until a final end point, e.g. death).	Unclear how risk factors execute 'force' (push) on marble; not clear what rolling up stands for (while rolling down is tb); normal behav. is not shown; not clear how tb incr. risk for subsequent tb (could be a lower second hill); not clear what represents the marble level (horizontal & vertical position).
D'Eath et al. (2014)	Tb	Flow chart	'Chaos'(?)	20 items connected by something like 35 arrows. Central item seems to be 'foraging activity'.	Differentiates between known and hypothesised relationships.	Rather chaotic figure with little intuitive appeal.

Van Niekerk (2015)	Fp	Equilibrium	Balance	Balance between environment and animal-based (stress) factors.	Problem of fp is represented as a disbalance; many factors can load on the scale.	Not clear what constitutes the balance (i.e. what loads on one scale and what on the other; not envir. vs animal-based; neither pos. vs neg. factors).
Boumans et al. (2016)	Tb	Agent-based model	Counter/'bucket' & threshold	Agent-based models simulate (more) complex group behaviour and output parameters based on (relatively simple) decision rules specified for (individual) agents (e.g. pigs). Each time step the pig's motivation may incr./decr. resulting in behav. when a threshold level is reached.	Feeding model produces (complex) output resembling reality.	Not (yet) suitable for a complex problem like fp/tb (not quantified enough?; better results were obtained for agent-based modelling of feed intake, dominance & personality (Boumans, 2017).
Brunberg et al. (2016)	Fp &tb	Framework	Envelope (?)	Development of fp/tb affected by species and individual characteristics as well as the physical and social environment (via (?) 'thwarted exploratory behaviour').	Distinguishes 3 types of animals (victim, performer, neutral/successful coper).	Model not clear without reading the (scientific) text; does not show how/why fp/tb escalates and/or state change takes place.
Zonderland (Bracke, 2017)	Tb	Communicating vessels	Communicating vessels	Water volume is (more or less) constant & represents (overall) explor. behav.; explorable objects are different containers with variable width (depending on suitability for the animal, modulated by other risk factors); water level in separate container indicates (risk for) fp/tb.	Some empirical support in pigs (Bracke, 2017).	Not clear what constitutes state change after onset of tb (may be modulation of own container width); no pos. feed forward (escalation); not intuitively appealing.
Bracke (new)	Fp &tb	Homeostatic	Face	Left ear: Multifactorial risk factors; Right ear; responses; 2 eyes: actor & victim; glasses: pos. & neg. feedback; nose: farmer; mouth: neutral; necklace: various alternative comparators (e.g. bucket, balance, etc.).	Includes the 3 different types of animal (actor, victim and neutrals) as well as the farmer (as a similar & crucial element in the development (prevention & treatment) of fp/tb).	'Face' does not have a functional meaning; figure does not make clear what is the main problem (outbreak of fp/tb) or its state change; does not show relationship between different needs.

Some model illustrations.

Since copy-rights are a problem for representing models, below a selection is given of models for which Wageningen UR (already) has the copy-rights. Other models can be obtained via the cited references or the internet. E.g. an example of the psychohydraulic model (Lorenz, 1950; 1978) can be found here.

Figure 7.3 below shows the tail biting (tb) model by Zonderland (2010a) (Fig. 7.3, p. 138).

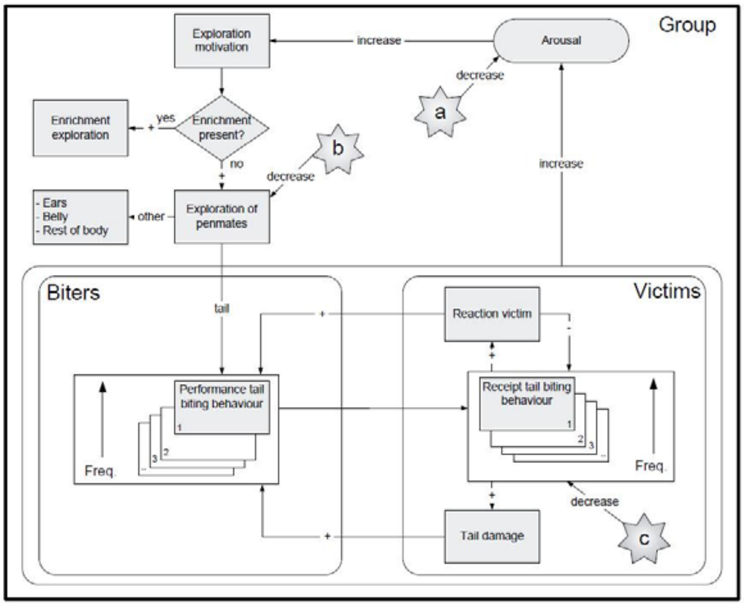

Figure 7.3 Aetiology model with exploration motivation leading to tail biting behaviour and tail damage in a group of pigs (+ = increased chance; - = decreased chance), including key points for preventive measures (a, b and c).

The conceptual framework for tb originating from Bracke (2008) (reprinted in (Bracke, 2017)) is shown in Figure 1 below. This model was designed to construct the RICHPIG model (decision support system) to assess/calculate the welfare value of enrichment materials for pigs.

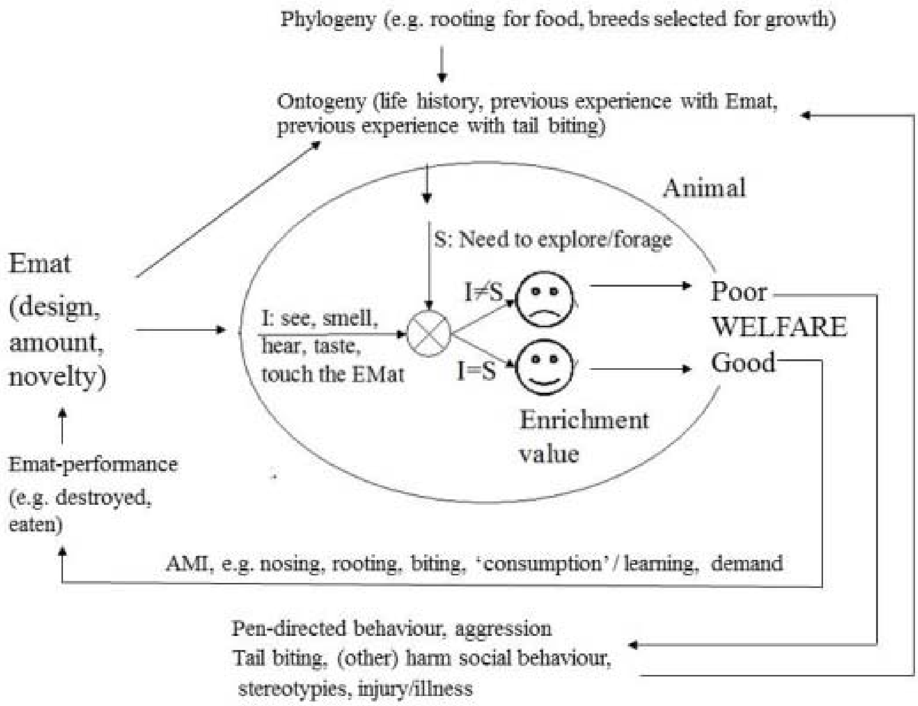

Figure 1. Schematic representation of the conceptual framework for assessing environmental enrichment for pigs. EMat: Enrichment material; AMI: animal-material interactions; I: Istwert, the environment as perceived by the animal; S: Sollwert, set point or norm (modified homeostatic model after Wiepkema (1987) and (Anonymous, 2001)). (Figure from Bracke (2008), permission granted by UFAW) (reprinted from (Bracke, 2017)).

Citation from Bracke (2017) relating the model to the principle of **communicating vessels**: "*Progressive feedback loops in the framework indicate that the animal's welfare is good when proper enrichment satisfies the pigs' need to explore and forage. When the enrichment is deficient, the animals will redirect their attention and show pen- and pen-mate directed behaviour. Note that this may imply a mechanism resembling the principle of* ***communicating vessels*** *(connected containers filled with liquid; see Wikipedia (2016c)). In accordance with this principle pigs may distribute their (motivation for) exploratory behaviour (the liquid) depending on the quality of the manipulable 'materials' available to them (cf Bracke et al. (2012)). Eventually, an outbreak of tail biting may occur, potentially evoking a positive feedback loop (an escalating outbreak) leading to cannibalism when no 'proper enrichment' is provided buffering and/or eliminating the (primary) cause/stressor.*" (End of citation).

In the communicating-vessels model, for which we found some empirical evidence in pigs (Bracke, 2017), vessel size may change due to animal-properties like genetics; but also e.g. enrichment-based and other risk factors.

In the case of fp in poultry, in a classic paper Newberry et al. (2007) questioned the assumption of communicating vessels underlying the hypothesis that fp is redirected foraging behaviour as proposed earlier by Blokhuis (1986). Newberry et al. (2007) showed that birds with high levels of ground pecking as chicks were more likely to develop high levels of fp as adults compared to low ground pecking chicks. However, the high ground pecking chicks also

continued to show high levels of ground pecking as adults, shedding doubt on the theory that fp would replace ground pecking.
Under 'mechanism' Van Niekerk (2015) presents both a balance model and a tipping-bucket model for fp (see also Van Niekerk (In prep.)). The bucket model was modified from a tb model originally proposed by Vermeer in Bracke et al. (2012). The main problem of the tipping-bucket model is that it suggests that fp/tb cannot stop, cannot be made undone (or perhaps only via an external 'force', e.g. a farmer taking adequate measures to correct the problem). Perhaps the model could be improved, e.g. by making a **tumbler-type tipping bucket**, such that it can be emptied, and then may restore its original position. However, this revised tumbler model would still be deficient in that post fp/tb set points are not the same as before (as a tumbler would suggest). Another option might be a **series of buckets**. Once tipped, the next bucket could stay down, with the next bucket being smaller, such that the next tipping point would be reached sooner, with preventive measures reducing the flow of water into the bucket. This would solve the issues just mentioned, but it would seem to be a somewhat 'artificial'/non-parsimonious model.

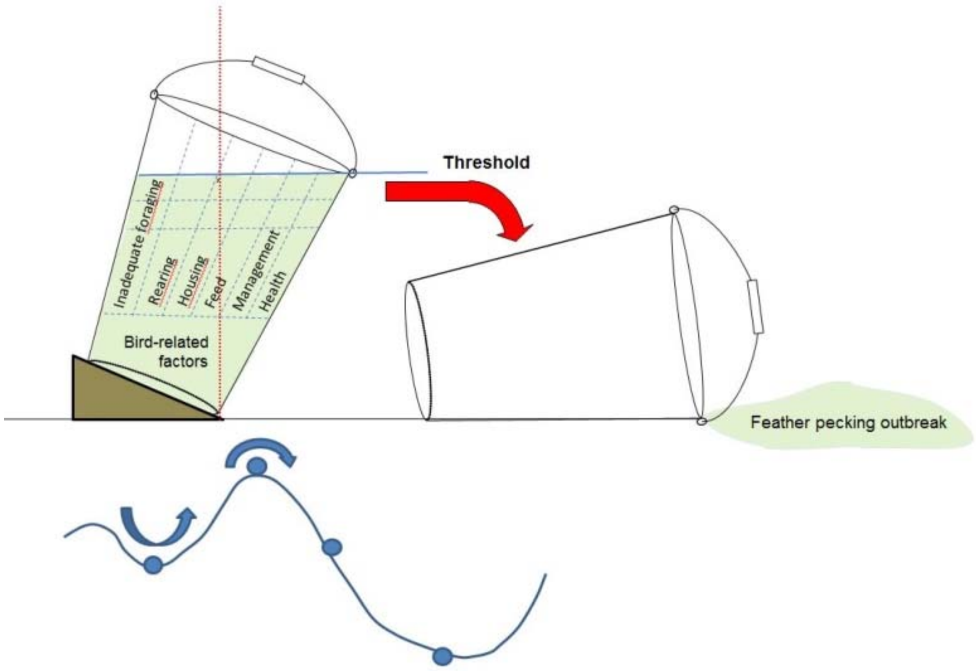

Figure 2. Tipping-bucket model of feather pecking (Van Niekerk (2015); modified after Bracke et al. (2012)).

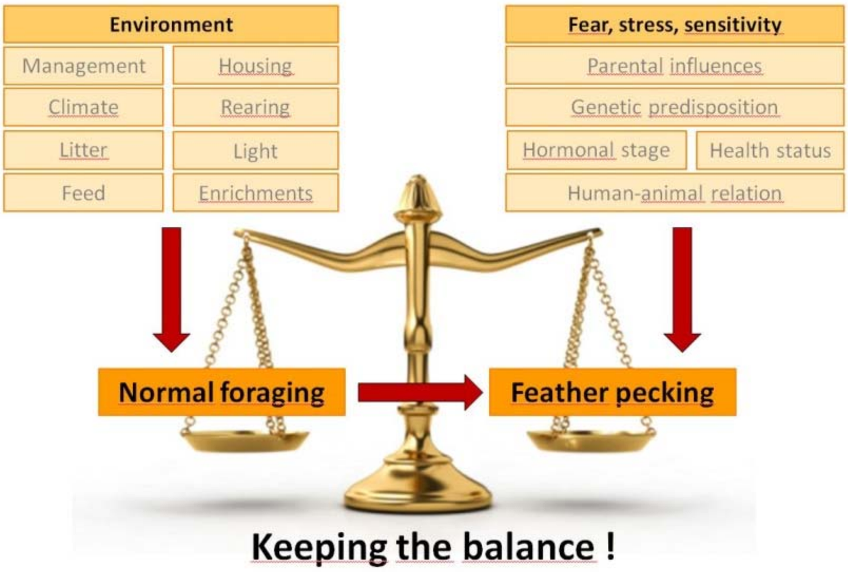

Figure 3. Balance model (Van Niekerk (2015), from http://www.henhub.eu/fp/mech/).

Perhaps the balance model could be modified to a balance between 'fixed' risk factors on the one scale and management (farmer effort) to reduce tb/fp risk on the other scale of the balance. However, the symmetry in disbalance suggested by the model does not seem to make sense: too much pressure on one side does not have the same effect as too much pressure on the other side. Also, fp/tb does not seem to be (totally) reversible: inducing fp/tb by removing a bit of enrichment cannot be undone by adding the same bit of enrichment (at least not shown). Also, to date no studies are available showing reversibility by adding other factors (e.g. inducing tb/fp by poor litter quality and then ‘treating’ this problem by adding e.g. better feed, etc.).

The next figure (Figure 4 below) shows a newly developed **‘face’ model** aimed at incorporating the different types of animal involved (actor, victim, neutral), as well as emphasising the role of the farmer (as a kind of ‘actor’) in dealing with a fp/tb problem. The farmer is important for prevention and treatment of fp/tb. The emergence of an animal-actor is necessary to start fp/tb, but the responsiveness of the victim also plays a roll. For example, a victim may more or less effectively avoid becoming a victim and respond more or less in a way that leads to escalation of an outbreak. While a learning process may have transformed actors into individuals predisposed to show the abnormal fp/tb behaviour again at a later stage, similarly, at some point victims may show learned helplessness (which may also more or less permanently alter their behavioural predisposition).

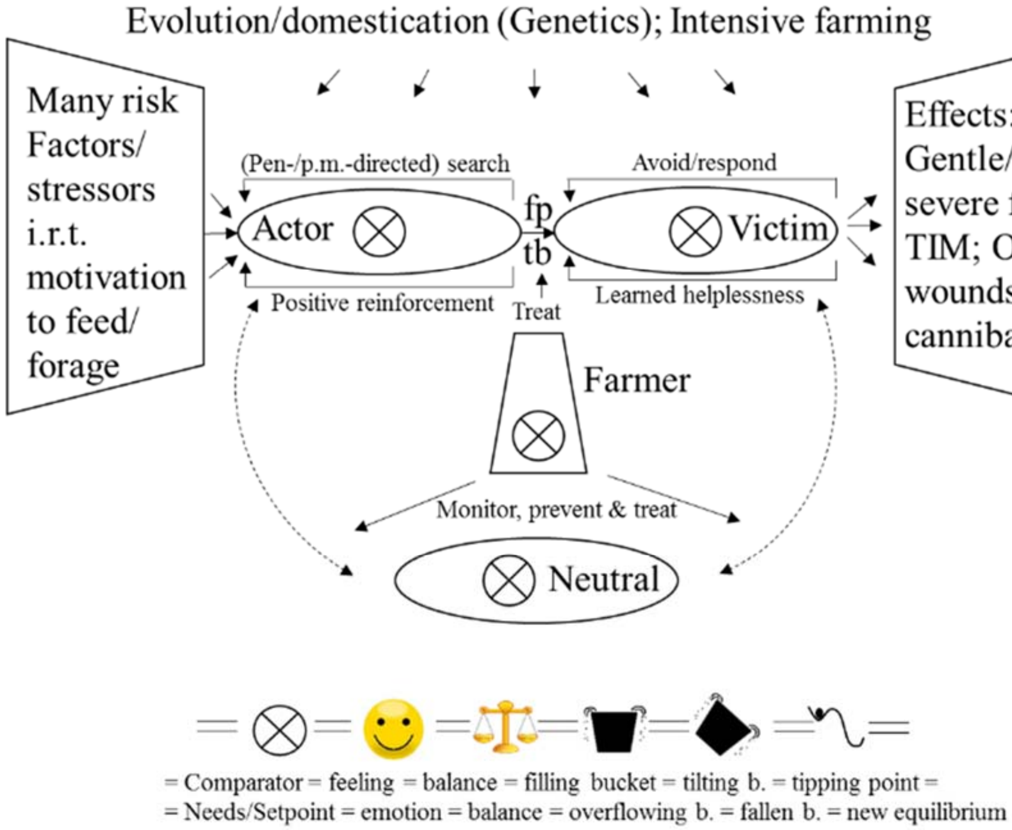

Figure 4. New 'face' model of feather pecking (fp)/tail biting (tb), showing its multifactorial nature ('left ear'), the role of different types of animal (actor & victim ('eyes'), neutral ('mouth')), array of responses ('right ear'), as well as the role of the farmer ('nose') in dealing with the problem. Both positive and negative feedback loops ('glasses' around the eyes of the face) are involved. Evolution and life history ('hairs') determine the set points of the individuals (animals and farmer). The comparators ('pupils' etc.) are (more or less) equivalent to welfare (smiley, balance, bucket and marble run) as indicated in the 'necklace' below the face. TIM: tail in mouth; OCTB: obsessive-compulsive tail biting; p.m.: pen mate; i.r.t.: in relation to. (Modified after (Bracke, 2017), and incorporating elements of the other models shown above, i.c. the balance and bucket models).

6. Disease framework

Brunberg et al. (2016) characterise feather pecking (fp)/tail biting (tb) as an abnormal behaviour. However, they do not frame it as a disease. This section deals with the question whether fp/tb may/should be regarded as a disease, i.e. as a medical disorder, in particular a mental/behavioural pathology.

Of course, a lesion of the bitten/pecked animal (victim) can be regarded as a health disorder. However, when fp/tb is primarily seen as a behaviour of the actor, and not as a medical disorder, then adequately understanding the behaviour requires addressing the 4 why questions proposed by Tinbergen (1963). That is, a behaviour is sufficiently understood if we understand its mechanism/causation, its function/adaptation, its evolution/phylogeny (over generations) and its development/ontogeny (over the course of the individual's life).

These aspects have been covered for the most part by Brunberg et al. (2016). However, aspects related to the importance and treatment of fp/tb were only marginally addressed.

When we were looking for a format to present the available information about fp at the www.henhub.eu/fp website, which was intended to inform farmers and the public, we decided to use the framework commonly used to describe medical disorders (Van Niekerk, 2015). This implies a characterisation of aspects like signs/symptoms/diagnosis (kinds of fp/tb), pathophysiology (mechanism), prevention, treatment and (economic) importance of fp. Aspects related to (differential) diagnosis and pathophysiology may, for example, deal with the question whether ear biting, ear necrosis and flank biting are to be regarded as forms of (i.e. having a causation (and treatment) similar to) 'tail biting. Conversely, Taylor et al. (2010) identified three types of tb in pigs: two-stage, sudden forceful and fanatic. These may be 3 different syndromes, all labelled 'tb'.

The importance of the fp/tb problem does not only concern production losses and financial implications. It may also concern legal, psychological and ethical aspects such as animal integrity, the attitude regarding 'blood' in the pen, aversion to sustainability pressures among farmers, e.g. due to fear of (over-)regulation. As to the legal relevance, both tail docking and beak trimming have been banned in the EU some time ago, yet despite this farmers have mostly continued to perform these procedures routinely (and they were repeatedly being granted exemption to do so).

Once fp/tb is regarded as a problem that needs to be solved, the disease framework clearly has added value. For example, it is important to realise/understand that the management of risk factors applied for the purpose of prevention of fp/tb is not necessarily the same as applying them for the purpose of curative treatment, i.e. counteracting an outbreak of fp/tb. E.g. it is likely that more enrichment is needed to treat than to prevent fp/tb.

In the commercial practice of intensive livestock farming fp/tb are common problems, esp. when routine mutilations were no longer allowed. However, that does not imply that it is normal for the animals involved to show such abnormal behaviours. Fp/tb have been labelled so-called technopathies, i.e. pathological behaviours associated with agro-technologically designed living conditions. A common perception among applied ethologists, namely, is that there is a wide discrepancy between the animals' living conditions in intensive livestock farming and the animals' environment of evolutionary adaptation. That is, the living conditions are not normal. They are likely to overtax the animals' control systems, thus leading to behavioural pathology/disorders. From an evolutionary perspective fp/tb is not part of the adaptive behaviours in which poultry/pigs deal with a variable environment. Instead these abnormal and injurious behaviours result from a frustrated need to perform rather species-specific foraging behaviours (scratching/rooting) for substantial periods of time, leading to boredom in relatively barren environments imposed under intensive livestock conditions.

The fact that these mutilating, harmful social behaviours (fp/tb) also (seem to) require preventive surgical interventions/mutilations (beak treatment, tail docking) strongly indicates that the label 'medical disorder' would seem to be appropriate. In humans self-harm and harmful social behaviour have been classified as (symptoms of) medical disorders, e.g. self-mutilation in borderline patients and antisocial/dissocial personality disorder respectively. Preventive mutilation also implies an infringement of the animals' integrity (a moral concern). It also indicates that the environment is not suited for the animals. Examples of preventive mutilations in human medicine are (religious) circumcision (e.g. for religious reasons or to prevent HIV in sub-Saharan Africa (Siegfried et al., 2009)), preventive mastectomy in women who are BRCA1 or BRCA2 mutation gene carriers (Zagouri et al., 2013), and prophylactic colectomy or even Whipple procedure (a major surgical operation involving the removal of the head of the pancreas, the duodenum, the proximal jejunum, gallbladder, and part of the stomach), e.g. in case of familial adenomatous polyposis (i.e. to prevent intestinal cancer). Whether in humans or animals, preventive surgery, even if intended to prevent 'greater harm'

later in life, is not to be regarded as ‘normal’. E.g. in the case of pigs and laying hens the preventive mutilations have been associated with chronic ‘phantom’ pain because of neuroma formation (pigs: (Simonsen et al., 1991; Di Giminiani et al., 2017); poultry: (Gentle, 1986)). And, while the mutilation may solve the problem of future victims, in doing so it masks the problem (stress, mental pathology) that gives rise to neutrals becoming actors that engage in destructive, harmful social (or sometimes self-mutilating (van Zeeland et al., 2009)) behaviours. To paraphrase an early Dutch researcher of tail biting in pigs, Gerrit van Putten: the pig's tail is a thermometer of animal welfare, which was discarded when the "temperature" became too high, i.e. the tails were docked rather than that housing conditions were improved. Also regarding the practice of preventing fp/tb using routine mutilations, it has been pointed out that these procedures are not fully effective. E.g. Zonderland et al. (2011) estimated a prevalence of 2.12% tail biting despite (very short) tail docking on Dutch farms.
Another indicator for viewing fp/tb as a medical disorder is the fact that fp/tb outbreaks lead to injuries (wounds), which may even escalate into cannibalism and/or death due to secondary infections of the wounds. This (progressive) loss of normal functioning and lack of homeostasis have typically been regarded as indicative of disease, esp. since these are also of economic significance to the farmers (Zonderland et al., 2011).
However, fp/tb is not just a problem because of wounds inflicted on the victims. As Brunberg et al. (2016) rightly point out, the (acute pain of the) victim is not the only welfare concern. An important part of the (more chronic) welfare problem concerns the stressors/behavioural deprivations that lead neutral animals to become actors of fp/tb. Fp/tb, therefore, is not just a medial disorder because of the clinical wounds (and surgical prevention practices), but also because of the likely mental disorder leading to the abnormal fp/tb behaviour shown by the actors. Taylor et al. (2010) distinguished three types of tail-biting pigs: two-stage (where tail biting is preceded by more gentle tail-in-mouth (TIM) behaviour), sudden forceful (without prior TIM, e.g. to get access to the feeder) and fanatic tb. The latter was also labelled as ‘obsessive’ and ‘persistent’, and may thus be classified tentatively as an ‘obsessive-compulsive’, which seems to come close to labelling this type of tb as an obsessive-compulsive mental disorder.
Formerly, harmful social behaviours like fp and tb have been labelled as ‘vices’. However, that label implies seeing the actors as a kind of criminals. In fact, and esp. the medical framework, would turn the actor into a kind of victim too, i.e. a victim of inappropriate/depriving/stressful living conditions of intensive farming.
A related point indicative of fp/tb being a medical disorder is the fact that fp/tb problems tend to spread in a pen (and perhaps also across pens). This may make fp/tb resemble an infectious disease/epidemic. In other words, fp/tb has disease-like properties: the behaviour has a tendency to escalate into a fp/tb outbreak. While it may be that novelty and reward (the taste of blood) may account for the frantic and ‘contagious’ appearance, the behaviour seems to be ‘contagious’, in that other animals in a pen/enclosure may acquire the behaviour once the first animal has started to engage in it. In this respect, it may be noted, that esp. in pigs often the pen is regarded as an ‘experimental unit’, while it remains to be shown that pigs in neighbouring pens remain unaffected by (the arousal caused by) ongoing tb.
A further disease-like property of fp/tb is the role of stress in the aetiology of the problem. Many diseases are aggravated by common stressors like high stocking densities and limited access of food or a poor climate, e.g. because stress may reduce the immune response needed to combat the disease. Similar stressors also play a role in triggering fp/tb. However, the underlying pathophysiological mechanism may not be the same, as stimulation of the (humoral) immune response has been shown to predispose (rather than inhibit) fp in laying hens (Parmentier et al., 2009).

Finally, it may be pointed out that most major textbooks describing the diseases of poultry/laying hens and swine/pigs already have a chapter or section on fp and tb respectively. In that respect, a start has been made to recognise fp and tb as a medical/mental/behavioural pathology. The conclusion of this section, we believe, justifies a more proper recognition of fp/tb as a medical disorder, i.c. a mental disorder, in the future.

7. Evolution & domestication

This final post/section aims to emphasise that adopting a disease framework for feather pecking (fp)/tail biting (tb) does not imply discarding the common science-based and evolutionary perspective on fp/tb. In order to show why this may be important we will first consider non-scientific reasoning to deal with fp/tb.

From a non-scientific and non-welfare perspective it may make perfect sense to farmers and veterinarians to prevent or treat fp/tb using respectively beak treatment (i.e. removing the means for fp) and tail docking (i.e. removing the object of tb). Similarly, measures like spectacles to prevent accurate vision (preventive measure in poultry) and teeth cutting (treatment measure in pigs) have been used, as has been the keeping of animals in the dark (thus blocking the animals' vision). Along these lines one may also propose breeding poultry without feathers and pigs without tails, hens with blunted beaks, and pigs without incisor teeth, or perhaps blind animals (Ali and Cheng, 1985) (e.g. without eyes). Similarly, physical restrictions may be imposed in theory, e.g. solitary confinement/individual housing would be highly effective in stopping fp/tb. A related 'solution' is a limited physical ability to move (rather than lack of motivation (Bokkers and Koene, 2004)), as appears to be the case in heavily selected broilers. In fact, this may (partly) explain why fp is much less of a problem in broilers compared to laying hens. When comparing broilers to pigs, another reason, besides the limited physical activity, may be age. Broilers are slaughtered at 5-6 weeks of age, while egg-laying (puberty) starts at around 17 weeks (when severe fp normally develops). In pigs slaughter age and puberty are around 6 months and tb may be seen roughly in the period between 4 weeks and 6 months. Perhaps the situation in pigs, where tb is frequently seen in weaned and young growing pigs, and in rearing gilts but not in pregnant/farrowing sows, is somewhat more comparable to turkeys, where fp is a problem (5-8% in untreated turkeys; 10-16% in beaktreated turkeys) at around 4 days of age and around 8-10 weeks of age, at which age egg-laying/puberty may also start, while slaughter age is around 16-20 weeks (Van Niekerk and Bracke, 2016; van Niekerk and Veldkamp, 2017). Turkeys, like pigs, have been bred less intensively for muscle growth compared to broilers (Van Niekerk and Bracke, 2016). However, it may also be noted that fp in turkeys does not seem to respond as favourably to enrichment as does fp in laying hens (Van Niekerk and Bracke, 2016) and tb in pigs. In line with these considerations, the comparison between fp in poultry (laying hens and broilers) and tb in weaned/growing pigs, would raise the tentative suggestion that while fp is less prevalent in fast-growing broilers because of their very young age and limited physical activity, slower-growing broilers, in virtue of the older age and enhanced physical activity, should be expected to have an enhanced propensity to show fp behaviour. An anonymous poultry-welfare expert (pers. comm.) indicates that this may indeed be the case.

A risk of using breeding for inactivity to reduce fp/tb, of course, could be that in addition to reducing the propensity of the actor to show harmful social behaviour, inactivity may also reduce the propensity of the victim to avoid being pecked/bitten. Another breeding goal may thus be to select for animals that do not have the (cognitive) capacity to 'discover' fp/tb, and/or to breed against the ability to acquire the behaviour through social transmission (i.e. to learn from conspecifics who have become actors). Such selection for 'stupidity' is also unlikely to be effective, because both laying hens and pigs need a certain level of cognitive

functioning and synchronisation, e.g. to regulate access to limited resources like nest boxes and feeders (Boumans, 2017).
A major factor in causing fp/tb is the animals' motivation to explore/forage. Would it then make sense to select against this motivation per se?
In applied ethology it is commonly assumed that fp/tb are caused or at least mediated by a deprived motivation to forage. The idea is that poultry and pigs still have behavioural needs originating from evolution in a natural environment. Domestication is not perceived to have had a major attenuating effect, i.e. modern pigs and poultry are not (yet) adapted to intensive farming. The motivation to forage is still considerable because it was essential to survive in a natural environment spending considerable periods of time searching for food. Being generalist omnivores also implied these animals had relatively inquisitive natures to investigate a wide variety of potential food items under variable circumstances encountered in nature.
In fact, this attraction to novelty and eagerness to learn may well be sufficient to explain one of the most characteristic features of fp/tb, namely that a kind of irreversible state change occurs once the first fp/tb has taken place, and also that the problem has a certain tendency to escalate and is much more difficult to counteract later than it is to prevent it from occurring in the first place. A normal learning process can thus explain the difference in set point between animals who have never experienced fp/tb and those that have. No pathology need to be involved here.
Esp. pigs that are provided with novel enrichment materials clearly show 'fanatic', almost compulsive behaviours, except that the behavioural intensity tends to wear off readily (it is mostly a matter of a few quarters rather than hours that pigs spend on interacting with new enrichment materials). However, when the enrichment is slowly destructible (like soft wood), designed to fit the needs of the animal (e.g. branched chain design, (Bracke, 2017)) or provides (irregular) food rewards, e.g. as in the case of the Edinburgh foodball in pigs (releasing food pellets upon being rooted and thus moved around the pen (Young et al., 1994)), much more persistent (and less fanatic) interest may be observed. Pigs and poultry also clearly appreciate the taste of blood and (tail/feather/skin) tissue.
Note also that in addition to being potentially explained as a cognitive (learning) process, the escalation of fp/tb and (subsequent) state change may also be related to cognition and a tendency to show synchronised (feeding/exploration/activity) behaviour. A related potentially-involved mechanism could be the supposedly powerful tendency to show conformism, as suggested by De Waal in the case of primates (De Waal, 2016).
E.g. van de Waal et al. (2013) showed that green monkeys that had been trained to prefer maize of one colour, would unlearn their previous colour preference and acquire the colour preference of the group they had been introduced into. Similarly, mixing a less friendly primate species with a more friendly species, made the former much (4 times) more friendly (De Waal and Johanowicz, 1993). Uitdehaag et al. (2009) found that mixed housing of a more and less fearful strain of laying hens negatively affected fp and fear-related behaviour. Perhaps conformism may play a role in fp/tb in that once more and more individuals start to show the behaviour, other individuals may have a strong tendency to do the same. Thus conformism may explain (part of the escalation) by potentiation, but it cannot explain its origin (though it may explain why there is a reluctance to show fp/tb in a group that has never experienced it before). (Note: the origin may also be more or less accidental, e.g. McAdie and Keeling (2000) showed that (artificially) damaged feathers may trigger (outbreaks of) fp in laying hens.)
Counteracting the motivation to show fp/tb by genetic selection may simultaneously counteract the animals' motivation to consume feed and thus (efficiently) produce under

commercial conditions. Pigs and poultry need to be eager to consume food and they must readily accept novel feeds (e.g. when moved from rearing farm to finishing/egg-laying farm). Thus, the motivation to forage may not only be a remnant of evolution in a natural environment, it may also be a product of selection for maximised production efficiency. In other words, domestication and genetic selection may have been co-shaping the current problem underlying fp/tb in intensive pig and poultry farming.

Traditionally, pigs and poultry have been selected using individual selection, i.e. the fastest growing individuals were selected to breed the next generation, perhaps even when individuals were showing high levels of production at the expense of pen mates (e.g. due to excessive aggression or the performance of fp/tb). In particular, when fp/tb occurred the (most heavily affected) victims were unlikely to be used for reproduction, but the actors in a pen could partly go unnoticed (unless they were detected and eliminated from the group). Group selection has been proposed as an alternative to individual selection, where the production efficiency of pen mates is also taken to load on an individual's selection potential (Muir, 2003; Bijma et al., 2007a; Bijma et al., 2007b). Group selection has thus been suggested as a potential solution for fp/tb by selecting for peaceful pigs/poultry. Such peaceful pigs, however, may be less motivated to forage, and thus be less efficient for production.

Genetic selection probably has made use of the evolutionary tendency of animals (esp. males) to grow fast so as to have a higher likelihood of reproduction (as the largest individuals of a generation tend to win fights for access to females). Fast growth (as required for pigs and broilers), however, requires a persistent appetite to sustain growth. Compared to egg-laying in hens, which similarly require a substantial appetite to be able to sustain a high egg production, the biological prioritisation is different. Resource allocation theory suggests that animals make adaptive adjustments in the allocation of resources to different life processes when facing changed selection pressures (Beilharz et al., 1993). Hens must prioritise allocating energy to their offspring (eggs), whereas pigs and broilers must (i.e. have been selected to) allocate energy to their own growth (so as to produce meat). Thus, both types of farm animals are also likely to have been selected to prioritise (as much as possible) those processes that are preferred by man (be it the production of meat or eggs). Thus, when dealing with (mild) disease states it is possible that farm animals have been selected to (tend to) prioritise production over the (energetically costly) activation of the immune response. Farm animals that continue 'functioning' in an economic/zootechnical sense, however, may not be the most productive overall, e.g. when enhanced appetite has a negative side-effect in increasing the likelihood of fp/tb.

Several observations may be in line with the suggestion that in modern farm animals appetitive foraging motivation may have originated in a discrepancy with the natural environment, but may also have been co-determined by genetic selection for maximised production efficiency. A main indicator is that adult animals, esp. pregnant sows and broiler breeders, are known to experience high levels of feeding motivation and a tendency to become obese when given ad lib access to feed. (In laying hens, however, fp rather seems to be associated with hyper-mobility, also called a hyperactivity disorder (Kjaer, 2009), perhaps related to an (over-)activated foraging motivation.) In addition, when growing pigs are feeding they seem to be focussed so much on feed intake that vaccinating them with a rather painful (large diameter) needle seems to go (largely) unnoticed. Also, growing pigs whose front teeth have been cut so as to counteract an outbreak of tail biting don't seem to show a clear reduction in feed intake. When their teeth have been cut, however, the pigs are much less inclined to continue tail biting and they also show much less interest in manipulating enrichment materials like chains, wood and ropes, suggesting that they do feel pain while maintaining a relatively high motivation to feed.

A final aspect where a science-based evolutionary understanding of fp/tb behaviour has clear added value over a classic medical framework may be the observation that not all kinds of stressors are equally likely to contribute to fp/tb. This may be an important aspect of the pathophysiology/mechanism underlying fp/tb. In laying hens, for example, organic farmers say that pullets with access to an outdoor range are less fearful later in life (e.g. in using the outdoor range), and therefore are less likely to develop fp (TvN, pers. comm.). Also in laying hens, the stressor of being moved from the rearing farm to the layer facility appears to be a trigger of stress and fp (even though it may also be a 'revival' of fp that originated at the rearing farm). In pigs, by contrast, mixing is not typically eliciting tail biting, despite the fact that it is highly stressful for the pigs. E.g. Holinger (2017) found no effect of mixing and isolation stress on tail and ear manipulation in pigs. Note also that mixing in pigs typically occurs at 25kg body weight (10-12 weeks of age), which is long before puberty at slaughter age, i.e. about 5-6 months of age, whereas laying hens are transferred to the laying facilities shortly before egg-laying starts (i.e. puberty). In pigs this compares to the rearing of breeding gilts, who are also particularly prone to tb (probably because they are fed on more restricted diets than slaughter pigs are), but only at a younger age (i.e. before the gilts are inseminated). Tb in pigs is hardly seen in (first or older parity) pregnant sows and in this respect tb in pigs differs from fp in laying hens. Such differences must be kept in mind, but they should not overrule the striking similarities between fp in poultry and tb in pigs, nor should they be regarded as a counterargument to the proposition that fp/tb would certainly benefit from being regarded as a medical/mental health disorder, provided the existing science-based and evolutionary framework is maintained to understand the behavioural as well.

Acknowledgements
This paper has been made possible by the Hennovation project (HORIZON 2020 ISIB-02-2014 project, Grant no. 652638).

8. References

Ali, A., Cheng, K.M., 1985. Early egg production in genetically blind (rc/rc) chickens in comparison with sighted (Rc+/rc) controls. Poultry science 64, 789-794.

Anonymous, 2001. Scientists' Assessment of the Impact of Housing and Management on Animal Welfare. Journal of Applied Animal Welfare Science 4, 3-52.

Beilharz, R., Luxford, B., Wilkinson, J., 1993. Quantitative genetics and evolution: is our understanding of genetics sufficient to explain evolution? Journal of Animal Breeding and Genetics 110, 161-170.

Bijma, P., Muir, W.M., Ellen, E.D., Wolf, J.B., Van Arendonk, J.A., 2007b. Multilevel selection 2: estimating the genetic parameters determining inheritance and response to selection. Genetics 175, 289-299.

Bijma, P., Muir, W.M., Van Arendonk, J.A., 2007a. Multilevel selection 1: quantitative genetics of inheritance and response to selection. Genetics 175, 277-288.

Blokhuis, H., 1986. Feather-pecking in poultry: its relation with ground-pecking. Applied Animal Behaviour Science 16, 63-67.

Bokkers, E.A., Koene, P., 2004. Motivation and ability to walk for a food reward in fast-and slow-growing broilers to 12 weeks of age. Behavioural Processes 67, 121-130.

Boumans, I.J., 2017. Simulating pigs - Understanding their motivation, behaviour, welfare and productivity, Wageningen University, Wageningen.

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

Bracke, M.B.M., 2008. Richpig: a semantic model to assess enrichment materials for pigs. Animal Welfare 17, 289-7286.
Bracke, M.B.M., 2017. Chains as proper enrichment for intensively-farmed pigs?, in: Spinka, M. (Ed.), Advances in Pig Welfare, Elsevier, pp. 167-197.
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, 31-44.
Bracke, M.B.M., Vermeer, H., Bokma, M., Van der Peet, C., Bolhuis, L., Leeijen, J., 2012. Checklist aanpak staartbijten bij (biologische) varkens. [Checklist dealing with tail biting in (organic) pigs] Flyer. Available: http://edepot.wur.nl/220045. Accessed 11-5-2016, Wageningen Livestock Research, Lelystad.
Brunberg, E.I., Rodenburg, T.B., Rydhmer, L., Kjaer, J.B., Jensen, P., Keeling, L.J., 2016. Omnivores going astray: a review and new synthesis of abnormal behavior in pigs and laying hens. Frontiers in veterinary science 3.
Camerlink, I., Ursinus, W.W., Bijma, P., Kemp, B., Bolhuis, J.E., 2015. Indirect genetic effects for growth rate in domestic pigs alter aggressive and manipulative biting behaviour. Behavior genetics 45, 117-126.
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? 8, 1479-1497.
Daigle, C.L., Rodenburg, T.B., Bolhuis, J.E., Swanson, J.C., Siegford, J.M., 2015. Individual consistency of feather pecking behavior in laying hens: once a feather pecker always a feather pecker? Frontiers in veterinary science 2, 6.
De Waal, F., 2016. Are we smart enough to know how smart animals are? WW Norton & Company.
De Waal, F., Johanowicz, D.L., 1993. Modification of reconciliation behavior through social experience: an experiment with two macaque species. Child development 64, 897-908.
Di Giminiani, P., Edwards, S.A., Malcolm, E.M., Leach, M.C., Herskin, M.S., Sandercock, D.A., 2017. Characterization of short-and long-term mechanical sensitisation following surgical tail amputation in pigs. Scientific Reports 7.
EFSA, 2007b. The risks associated with tail biting in pigs and possible means to reduce the need for tail docking considering the different housing and husbandry systems. Available: http://www.efsa.europa.eu/en/efsajournal/doc/611.pdf. Accessed 10-5-2016, EFSA, Parma, Italy.
Folkedal, O., Pettersen, J., Bracke, M., Stien, L., Nilsson, J., Martins, C., Breck, O., Midtlyng, P., Kristiansen, T., 2016. On-farm evaluation of the Salmon Welfare Index Model (SWIM 1.0): theoretical and practical considerations. Animal Welfare 25, 135-149.
Fraser, D., 1987a. Mineral-deficient diets and the pig's attraction to blood: implications for tail-biting. Canadian Journal of Animal Science 67, 909-918.
Gentle, M., 1986. Neuroma formation following partial beak amputation (beak trimming) in the chicken. Research in Veterinary Science 41, 383-385.
Holinger, M., 2017. Does chronic intermittent stress increase tail and ear manipulation in pigs?, From beak to tail – Mechanisms underlying damaging behaviour in laying hens and pigs (Satellite workshop ISAE-2017), Aarhus, Denmark.
Hughes, B., Duncan, I., 1988. The notion of ethological 'need', models of motivation and animal welfare. Animal Behaviour 36, 1696-1707.
Kjaer, J.B., 2009. Feather pecking in domestic fowl is genetically related to locomotor activity levels: implications for a hyperactivity disorder model of feather pecking. Behavior genetics 39, 564-570.

Korte, S.M., Olivier, B., Koolhaas, J.M., 2007. A new animal welfare concept based on allostasis. Physiology & behavior 92, 422-428.
Lorenz, K., 1978. Vergleichende Verhaltensforschung: Grundlagen der Ethologie. Springer-Verlag., Vienna.
Lorenz, K.Z., 1950. The comparative method in studying innate behavior patterns, Symposium of the Society of Experimental Biology, pp. 221–268.
McAdie, T.M., Keeling, L., 2000. Effect of manipulating feathers of laying hens on the incidence of feather pecking and cannibalism. Applied Animal Behaviour Science 68, 215-229.
Muir, W.M., 2003. Indirect selection for improvement of animal well-being., pp. 247–256 in Poultry Genetics Breeding and Biotechnology, edited by W. M. Muir and S. Aggrey. CABI Press, Cambridge, MA.
Newberry, R.C., Keeling, L.J., Estevez, I., Bilčík, B., 2007. Behaviour when young as a predictor of severe feather pecking in adult laying hens: the redirected foraging hypothesis revisited. Applied Animal Behaviour Science 107, 262-274.
Nicol, C., Bestman, M., Gilani, A., De Haas, E., De Jong, I., Lambton, S., Wagenaar, J., Weeks, C., Rodenburg, T., 2013. The prevention and control of feather pecking: application to commercial systems. World's Poultry Science Journal 69, 775-788.
Noble, C., Jones, H.A.C., Damsgård, B., Flood, M.J., Midling, K.Ø., Roque, A., Sæther, B.-S., Cottee, S.Y., 2012. Injuries and deformities in fish: their potential impacts upon aquacultural production and welfare. Fish physiology and biochemistry 38, 61-83.
Parmentier, H., Rodenburg, T., De Vries Reilingh, G., Beerda, B., Kemp, B., 2009. Does enhancement of specific immune responses predispose laying hens for feather pecking? Poultry science 88, 536-542.
Pettersen, J.M., Bracke, M.B.M., Midtlyng, P.J., Folkedal, O., Stien, L.H., Steffenak, H., Kristiansen, T.S., 2014. Salmon welfare index model 2.0: an extended model for overall welfare assessment of caged Atlantic salmon, based on a review of selected welfare indicators and intended for fish health professionals.
Rodenburg, T., Van Krimpen, M., De Jong, I., De Haas, E., Kops, M., Riedstra, B., Nordquist, R., Wagenaar, J., Bestman, M., Nicol, C., 2013. The prevention and control of feather pecking in laying hens: identifying the underlying principles. World's Poultry Science Journal 69, 361-374.
Rodenburg, T.B., Komen, H., Ellen, E.D., Uitdehaag, K.A., van Arendonk, J.A., 2008. Selection method and early-life history affect behavioural development, feather pecking and cannibalism in laying hens: a review. Applied Animal Behaviour Science 110, 217-228.
Schrøder-Petersen, D.L., Simonsen, H., 2001. Tail biting in pigs. The Veterinary Journal 162, 196-210.
Siegfried, N., Muller, M., Deeks, J.J., Volmink, J., 2009. Male circumcision for prevention of heterosexual acquisition of HIV in men. The Cochrane Library.
Simonsen, H., Klinken, L., Bindseil, E., 1991. Histopathology of intact and docked pigtails. British Veterinary Journal 147, 407-412.
Stien, L.H., Bracke, M.B.M., Folkedal, O., Nilsson, J., Oppedal, F., Torgersen, T., Kittilsen, S., Midtlyng, P.J., Vindas, M.A., Øverli, Ø., Kristiansen, T.S., 2013. Salmon Welfare Index Model (SWIM 1.0): a semantic model for overall welfare assessment of caged Atlantic salmon: review of the selected welfare indicators and model presentation, Reviews in Aquaculture, Oxford, UK, pp. 33-57.
Taylor, N.R., Main, D.C., Mendl, M., Edwards, S.A., 2010. Tail-biting: a new perspective. The Veterinary Journal 186, 137-147.
Tinbergen, N., 1963. On aims and methods of ethology. Ethology 20, 410-433.

Uexküll, J.v., 1909. Umwelt und innenleben der tiere, Springer, Berlin.
Uitdehaag, K.A., Rodenburg, T.B., Bolhuis, J.E., Decuypere, E., Komen, H., 2009. Mixed housing of different genetic lines of laying hens negatively affects feather pecking and fear related behaviour. Applied Animal Behaviour Science 116, 58-66.
Valros, A., 2017. Tail biting, in: Spinka, M. (Ed.), Advances in Pig Welfare, Elsevier.
Valros, A., Heinonen, M., 2015. Save the pig tail. Porcine Health Management 1.
van de Waal, E., Borgeaud, C., Whiten, A., 2013. Potent social learning and conformity shape a wild primate's foraging decisions. Science 340, 483-485.
Van Dooren, K., 2013. Hoofdrol varkenshouder bij voorkomen staartbijten. [Main role for pig farmer in preventing tail biting]. Jan. 13, 2013. Available: http://www.boerderij.nl/Varkenshouderij/Nieuws/2013/1/Hoofdrol-varkenshouder-bij-voorkomen-staartbijten-1157354W/. Accessed 13-5-2016, Boerderij.nl.
Van Niekerk, T., 2015. Overview feather pecking. Available at http://www.henhub.eu/fp/. Accessed 11-2-2018.
Van Niekerk, T., In prep. Evidence based management of injurious pecking, Poultry Science.
Van Niekerk, T., Bracke, M.B.M., 2016. Pikkerij bij kalkoenen - Een stap terug naar het natuurlijk gedrag en soortspecifieke eigenschappen [Pecking in turkeys - A step back to natural behaviour and species-specific characteristics], Wageningen Livestock Research, Wageningen.
van Niekerk, T.G.C.M., Veldkamp, T., 2017. Insects for turkeys, Wageningen Livestock Research, Wageningen.
van Zeeland, Y.R.A., Spruit, B.M., Rodenburg, T.B., Riedstra, B., van Hierden, Y.M., Buitenhuis, B., Korte, S.M., Lumeij, J.T., 2009. Feather damaging behaviour in parrots: A review with consideration of comparative aspects. Applied Animal Behaviour Science 121, 75-95.
Wiepkema, P.R., 1987. Behavioural aspects of stress, in: Wiepkema, P.R., Adrichem, P.W.M.v. (Eds.), Biology of stress in farm animals: an integrative approach, Martinus Nijhoff, Dordrecht, pp. 113-133.
Wikipedia, 2016c. Communicating Vessels. Available: https://en.wikipedia.org/wiki/Communicating_vessels. Accessed 8-9-2016.
Young, R.J., Carruthers, J., Lawrence, A.B., 1994. The effect of a foraging device (The 'Edinburgh Foodball') on the behaviour of pigs. Applied Animal Behaviour Science 39, 237-247.
Zagouri, F., Chrysikos, D.T., Sergentanis, T.N., Giannakopoulou, G., Zografos, C.G., Papadimitriou, C.A., Zografos, G.C., 2013. Prophylactic mastectomy: an appraisal. The American Surgeon 79, 205-212.
Zonderland, J.J., 2010a. Talking tails: quantifying the development of tail biting in pigs.
Zonderland, J.J., 2010b. Terug naar de Krulstaart, Veehouder en Dierenarts, pp. 21-23.
Zonderland, J.J., Bosma, A.J.J., Hoste, R., 2011. Financiële consequenties van staartbijten bij varkens. [Financial consequences of tail biting in pigs]. Report. Available: http://www.wageningenur.nl/en/Publication-details.htm?publicationId=publication-way-343134343230. Accessed 1-5-2016, Wageningen UR Livestock Research, Lelystad.
Zonderland, J.J., Zonderland-Thomassen, M.A., 2016. Behavioural change by pig producers is the key factor in raising pigs with intact tails. The Veterinary Journal 211, 1-2.