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The potential of feeding patterns to assess generic welfare in growing-finishing pigs

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ABSTRACT

The welfare of growing-finishing pigs is important inherently to the pigs, but also for the societal acceptance and environmental impact of the husbandry system. Nevertheless, methods to monitor pig welfare throughout the whole growing-finishing phase have not yet been successfully developed. One possibility is to use electronic feeding stations to identify the feeding pattern of individual pigs, which consists of feed intake and the behaviours underlying intake (*i.e.* feeding frequency, duration and rate), and to process this data using an algorithm that links feeding patterns to pig welfare. Before such a monitoring system can be developed, a thorough understanding of both pig feeding patterns and their relationships with pig welfare is required. The aim of this review was to assess the current state of this understanding. We begin with a narrative review that describes the feeding patterns of growing-finishing pigs, and subsequently provide a systematic review of the relationships between pig feeding patterns and welfare. We focused on animal-based parameters of pig welfare, but also included resource-based parameters known to influence welfare (*e.g.* space allowance, environmental enrichment). We found that so far, studies have focused on physiological and behavioural welfare problems, while the affective part of welfare, both positive and negative, has been largely overlooked. Deviations from basal feeding patterns may occur during reduced welfare states, sometimes even preceding other clinical or behavioural manifestations of the problem. Particularly clear are the links between feed intake and physiological causes of reduced welfare, such as clinical health, thermal stress and tail biting wounds. The behaviours underlying intake provide further information, as they show distinct deviations in response to different physiological welfare problems and as their rapid responses may enable detection of disease at a subclinical stage. However, a wider range of clinical diseases should be studied before this knowledge can be applied. Behavioural welfare problems, such as abnormal behaviours and feed competition, mostly induce deviations in the feeding behaviours underlying intake but not intake itself, though more knowledge is required to confirm this finding. We conclude that feeding patterns are a promising tool to monitor generic pig welfare. Feed intake and the behaviours that underlie it should be used simultaneously, on a short time scale (*i.e.* within the day). It should be considered that the variation in feeding patterns between and potentially within pigs is large, and that this variation should be well-understood before welfare-relevant variation can be interpreted.

1. Introduction

1.1. Background

The welfare of farm animals (hereafter referred to as animals) is important not only inherently for the animals, but also for the societal acceptance (Broom, 2010) and environmental impact (Chemineau, 2016) of husbandry systems. In growing-finishing pigs (for simplicity, 'pig' is used to refer to growing-finishing pigs, while reference to other types of pigs is additionally specified), welfare is mostly monitored by the farmer, who identifies clinical disease or behavioural problems and intervenes. With the long-standing increase in farm sizes (CBS, 2015), it becomes increasingly difficult for farmers to obtain a good picture of the welfare of each pig under their care. In addition, farmers are likely to only identify clinical disease and obvious behavioural deviations that require intervention, while other causes of reduced welfare, such as mild social stress or subclinical disease, may go unnoticed. To obtain a more detailed and complete picture of pig welfare, an external assessment,

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such as the Welfare Quality® protocol (Welfare Quality®, 2009), can be used. Although external assessments give more detail and provide information that could be communicated to internal and external parties, such as farmers, farm advisors and consumers, they only provide a snapshot in time and are very time consuming to perform. In addition, they often suffer from complex, unbalanced and subjective aggregations of different aspects of welfare to come to an overall welfare score (Czycholl et al., 2017; de Vries et al., 2013).

An alternative method comes from precision livestock farming (PLF), which could potentially enable continuous monitoring of (individual) pigs to rapidly identify reduced welfare states and gain knowledge on the welfare of each pig across its entire growing-finishing phase (Berckmans, 2014). For example, microphones can be used to detect respiratory disorders at group level (Guarino et al., 2008), and 3D cameras have been used to predict tail biting outbreaks by automatically identifying lowered tail postures (D`Eath et al., 2018). Another promising type of PLF technology monitors the feeding patterns of individual pigs, using electronic feeding stations, radio-frequency identification (RFID) antennas at the feeder or computer vision, although the latter two provide less detail than electronic feeding stations. As numerous relationships between feeding patterns and welfare aspects have been reported (*e.g.* with disease (Brown-Brandl et al., 2013; Munsterhjelm et al., 2015) and thermal stress (Brown-Brandl et al., 2000; Nienaber et al., 1996)), these feeding patterns could potentially be used to monitor pig welfare. Nevertheless, a thorough understanding of both pig feeding patterns themselves and their relationships with pig welfare should be available before that potential can be utilised.

1.2. Aim of the review

The aim of this review was to assess the current state of our understanding of pig feeding patterns and their relationships with pig welfare. This review consists of two parts: 1) a narrative review describing feeding patterns in pigs and their variation, and 2) a systematic review of the relationship between feeding patterns and several aspects of pig welfare. In the next section, we first describe the steps made to obtain and select the relevant literature. This is followed by the narrative and systematic reviews and, finally, a discussion integrates the acquired information and assesses whether a good coverage of the different aspects of pig welfare has been obtained.

2. Methods

This review consists of a narrative and a systematic literature search that were both completed by the first author on June 17th, 2020, and includes relevant articles published before that date. For both the narrative and the systematic review, the same searches were performed. However, for the systematic review the papers were processed and included systematically (n = 116), while for the narrative review a selection of the most relevant papers (n = 100) was made due to the high number of papers reporting similar results. The systematic part, which focused on the relationship between feeding patterns and pig welfare, used primarily animal-based indicators of welfare, and included resource-based indicators if these were known to be relevant for pig welfare, such as space allowance or environmental enrichment. Welfare was defined here as the balance between positive and negative experiences (*e.g.* Green and Mellor, 2011; Webb et al., 2019). Three searches were performed: 1) a wide, general search to identify papers on pig feeding patterns, and two narrower searches focused on either 2a) the relation between clinical health and pig feeding patterns or 2b) the relation between other aspects of negative or positive welfare and pig feeding patterns. All searches were performed using Topic search terms in Web of Science, and backward and forward snowballing were performed on the selected articles. Backward snowballing uses the reference list of a source article to identify additional articles, while forward snowballing identifies articles that cited the source article using the "cited by"-function of a search engine, here Google Scholar.

Search 1) used a search string consisting of three parts: "feeding pattern" AND "growing-finishing pigs" NOT "non-target animals". The exclusion was solely used to reduce the number of irrelevant results. The exact search string was: ("feed intake" OR "feeding duration" OR "feeding frequency" OR "feeding time" OR "feeding visit*" OR "feeder visit*" OR "feeding pattern" OR "feeding behavio*r") AND ("growing-finishing pig*" OR "growing pig*" OR "fattening pig*" OR gilt* OR barrow* OR boar* OR "meat pig*" OR grower* OR finisher*) NOT (broiler* OR cattle OR sheep OR goat* OR fish). From the resulting articles, only peer-reviewed articles in English, Dutch and German were selected, and reviews, meta-analyses, reprints, MSc theses, articles without full-text access and articles concerning other types of pigs or animals than growing-finishing pigs were excluded. For the remaining articles, relevance for inclusion in the systematic review was judged based on title, abstract and full-text relevance, in that order. Relevant articles included at least one parameter of feeding behaviour and compared this to either 1) animal-based parameters of pig welfare or 2) resource-based parameters that are known to influence pig welfare, such as space allowance or environmental enrichment. Backward and forward snowballing were performed on the resulting articles to identify additional articles, based on title relevance. Subsequently, these articles were subjected to the same inclusion criteria as during the original search.

To ensure that the first wide search had identified all papers relating (aspects of) feeding behaviour to pig welfare, and collect any articles not yet obtained, two additional, narrower searches were performed (2a & 2b). The search strings included the same three parts as during the first search, but added a fourth part that included 2a) a range of clinical diseases or 2b) a range of keywords for negative and positive welfare not related to clinical disease. The strings used were: 2a) AND (health OR disease OR injury OR pneumonia OR lameness OR lame OR bursitis OR diarrhoea OR diarrhea OR clinical OR subclinical OR pathogen OR lesion OR lesions OR hygiene OR cleanliness OR sanitary OR coughing OR sneezing OR pumping OR scouring OR wound OR wounds); and 2b) AND ("thermal stress" OR "heat stress" OR "cold stress" OR "high temperature" OR "low temperature" OR "social stress" OR dominance OR "rank order" OR competition OR "social facilitation" OR "tail biting" OR "abnormal behavio*r" OR "belly nosing" OR "positive welfare" OR "positive emotion" OR "positive mood" OR enrichment OR enriched OR straw). The resulting articles were processed using the same criteria as those of the first search, and forward and backward snowballing were performed in identical fashion. Only articles that had not yet been identified in the first search were included, otherwise these are marked as duplicates.

In total, 116 papers were included in the systematic review. An overview of the number of papers considered at each step of the selection process can be found in Fig. 1. Based on the contents of the included papers, six categories of welfare parameters were identified: clinical disease, subclinical disease, thermal stress, social behaviour, tail biting and environmental enrichment. In the systematic review, we discuss the literature for each welfare category separately. Each category also includes a table that summarises the results for the main feeding parameters: feed intake, and feeding duration, frequency and rate. Note that not all studies included in the systematic review may be present in these summary tables, as some were of a design that was not relevant for inclusion, such as modelling studies or results of behavioural tests. Most of the included studies observed feeding patterns in the home pen under *ad libitum* feeding, but some used restricted feeding or a behavioural test. A full overview of all articles included in the systematic review and their findings can be found in the Supplementary materials.

3. Feeding patterns in pigs

3.1. A description of pig feeding patterns

Pig feeding patterns consist primarily of feed intake and the

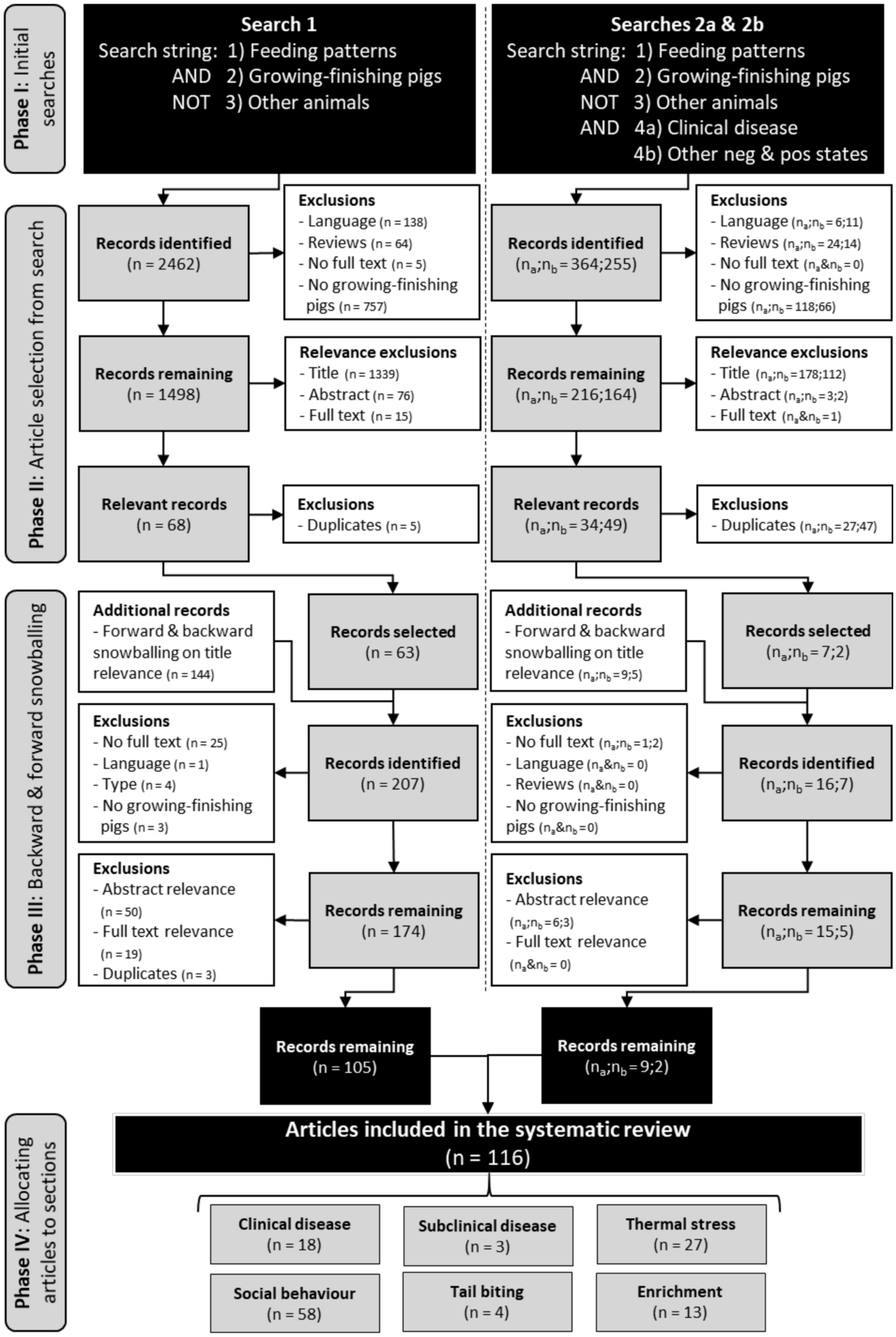

Fig. 1. A flow chart of the procedure of article selection for the systematic review, including the number of articles considered at every step.

behaviours that underlie intake: feeding frequency, duration and rate. Behaviourally, feeding rate is a driver of feed intake, but in practice it can only be estimated by dividing intake by duration. These parameters can be expressed on multiple time scales, such as per 24 h, per feeding visit or per meal. A visit is generally defined as every time a pig enters the feeder, while a meal is defined as an accumulation of sequential visits that were separated by an interval below a calculated meal criterion (Howie et al., 2009; Maselyne et al., 2015). The underlying assumption is that between rapidly successive visits the pig remains mentally occupied with feeding, as satiety has not yet been reached, and that, therefore, these visits should be considered as one feeding event: a meal. However, statistical methods to calculate meal criteria vary widely between authors and their biological relevance (*i.e.* what is the pig doing between visits?) is not always clear (reviewed by Maselyne et al., 2015). In addition to the basic parameters, the frequency of non-nutritive visits (*i.e.* when the pig visits the feeder but does not consume any feed) (Garrido-Izard et al., 2020; Young and Lawrence, 1994) and the interval between visits or between meals (Herrera-Cáceres et al., 2019; Kapun et al., 2017, 2016; Nienaber et al., 1991) are parameters contributing to feeding patterns. Some authors have also included additional parameters, such as time spent eating simultaneously with other pigs (Kapun et al., 2017) or time spent queuing for access to the feeder (Morrow and Walker, 1994a; Rasmussen et al., 2006a, 2006b; Walker, 1991).

The different feeding parameters are, as could logically be expected (Nielsen, 1999), strongly related to each other, where correlation coefficients of above 0.8 are repeatedly reported (Carcò et al., 2018; Von Felde et al., 1996). For example, at pig level it has been reported that a higher feed intake relates to a longer eating time (Guo et al., 2015b; Hyun and Ellis, 2002, 2000; Rauw et al., 2006; Schulze et al., 2001), that a lower feeding frequency relates to a higher intake and duration per visit (Carcò et al., 2018; Fernández et al., 2011; Garrido-Izard et al., 2020; Hall et al., 1999a; Hyun et al., 1997; Hyun and Ellis, 2002, 2000; Nielsen et al., 1995; Schamun and Hoy, 2011; Schulze et al., 2001; Young and Lawrence, 1994); and that a higher feeding rate relates to a higher feed intake per day and per visit and a lower daily feeding duration (Carcò et al., 2018; Chen et al., 2010; Garrido-Izard et al., 2020; Guo et al., 2015b; Herrera-Cáceres et al., 2019; Hyun and Ellis, 2002, 2000; Ragab et al., 2019; Schulze et al., 2001). These relationships between feeding parameters appear to have a genetic basis (Ding et al., 2018; Herrera-Cáceres et al., 2019; Labroue et al., 1997; Rohrer et al., 2013; Von Felde et al., 1996), and indicate that individual pigs have distinct behavioural strategies to achieve their desired nutritional intake (Fernández et al., 2011; Garrido-Izard et al., 2020). In support of the latter, it was reported that feeding patterns recorded at the beginning of the growing period correlated with those recorded at later stages on the same animals (Ragab et al., 2019; Rauw et al., 2006).

Nevertheless, feeding patterns are known to change with age. Many studies have reported that daily feed intake increases with body weight in a linear fashion, until a plateau in intake is reached (Casey, 2003; Fàbrega et al., 2003; Hauschild et al., 2020; Kavlak and Uimari, 2019; Labroue et al., 1999; Lorenzo Bermejo et al., 2003; Mensching et al., 2018; Morgan et al., 2000; Nielsen et al., 1995; Putz et al., 2019; Rauw et al., 2006). When exactly this plateau is reached can vary largely, with reported ages differing from 99 to 180 days (Fàbrega et al., 2003; Godcharles et al., 1993; Lorenzo Bermejo et al., 2003). Although increasing feed intake is initially mediated by increasing daily feeding duration (Hyun and Ellis, 2000; Rauw et al., 2006), feeding duration seems to later decrease with age (Hall et al., 1999b; Hyun and Ellis, 2000; Kavlak and Uimari, 2019; Labroue et al., 1999; Mensching et al., 2018; Rauw et al., 2006). In these later stages, the increase in feed intake is achieved through an increase in feeding rate (Hall et al., 1999b; Kavlak and Uimari, 2019; Labroue et al., 1999; Mensching et al., 2018; Quiniou et al., 2000a). Feeding rate increases because body size and oral capacity become larger over time, which allows pigs to take larger bites and eat more food in less time. Indeed, if feeding rate is expressed per kilogram of metabolic weight, it is seen to decrease rather than increase over time (Nienaber et al., 1991, 1990). Feeding frequency is generally reported to reduce over time (Hoy et al., 2012; Labroue et al., 1999, 1994; Quiniou et al., 2000a; Walker, 1991), while intake (Hall et al., 1999b; Hoy et al., 2012; Kavlak and Uimari, 2019; Mensching et al., 2018; Nienaber et al., 1990; Quiniou et al., 2000a) and duration (Nienaber et al., 1990; Walker, 1991) per visit or meal are reported to increase over time. This change to larger meals is likely a consequence of enlarging gut capacity (Boumans et al., 2015; Quiniou and Noblet, 2012).

If we look at the pattern of feeding behaviour within a day, under *ad libitum* feeding, an alternans pattern in feed intake can be identified (*e.g.* De Haer and Merks, 1992; Montgomery et al., 1978; Schouten, 1986). An alternans feeding pattern is characterised by a majority of feed intake occurring during the day, with a small peak in the morning and a larger peak in the afternoon (Fig. 2). Although this pattern is still weakly developed in young pigs, it becomes more distinct with age (Morrison et al., 2003; Toft and Madsen, 1998; Weiler et al., 2013). The peaks in feed intake coincide with peaks in feeding duration (*e.g.* Laitat et al., 2015; Renaudeau, 2009; Villagrá et al., 2007; Weiler et al., 2013) and frequency (*e.g.* Fernández et al., 2011; Garrido-Izard et al., 2020; Hoy et al., 2012; Xin et al., 2016; Young et al., 2011), while the opposite pattern is seen for feed intake and feeding duration per visit (Bigelow and Houpt, 1988; Chen et al., 2010; Hyun et al., 2001, 1997; Hyun and Ellis, 2001). This can be explained by a high level of competition at the feeder during peak hours, which leads to frequent displacements and thus many short feeding visits. Indeed, when the number of pigs per feeder and hence competition is low, no lower levels in intake and duration per visit during peak hours were seen (Hyun and Ellis, 2002). Feeding rate is reported to be quite constant throughout the day (Baumung et al., 2006; Feddes et al., 1989; Hyun et al., 2001), although it might increase during the afternoon peak (Andretta et al., 2016; Baumung et al., 2006; Feddes et al., 1989; Fernández et al., 2011; Garrido-Izard et al., 2020; Young and Lawrence, 1994). This implies that feeding rate is less easily adapted during competition than feeding frequency and duration. It should be noted that all patterns in feeding behaviours strongly depend on Zeitgebers, which are environmental factors that synchronise the internal circadian clock to real day length (Aschoff, 1966), such as the light-dark cycle, feeding times and caretaker activity. Of all possible Zeitgebers, the lighting regime appears particularly important, as application of continuous lighting causes the diurnal feeding pattern to collapse (Hsia and Wood-Gush, 1984a; Ingram et al., 1980), especially in individually-housed pigs (Ingram et al., 1980). Nevertheless, a weakened form of the diurnal pattern may still be maintained during continuous lighting if other Zeitgebers are present (Hyun et al., 1997).

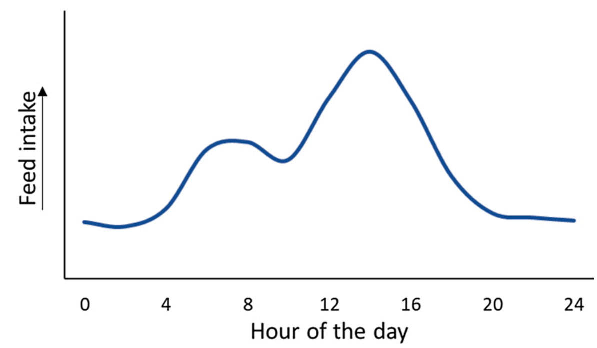

Fig. 2. The alternans diurnal pattern in feed intake shown by group-housed growing-finishing pigs, based on de Haer and Merks (1992), Schouten (1986) and Montgomery et al. (1978). Note that the exact timing of the peaks depends on the lighting regime applied, and that the results are shown at group level, averaged over time.

3.2. Variation in feeding patterns

It has repeatedly been acknowledged that the variation in feeding patterns, both within and between studies, is large. This is mainly the case for the underlying feeding behaviours, while variations reported for daily feed intake are much smaller (Ding et al., 2017). For example, the standard deviations of feeding frequency, duration and rate commonly reach values as high as a third of the group mean (Ding et al., 2017; Do et al., 2013b; Jiao, 2015; Maselyne et al., 2014). Moreover, only 16 % of animals were reported to show a daily feeding duration within one standard deviation of the mean (Andretta et al., 2016), and for all parameters pigs regularly showed values more than three standard deviations away from the mean (Reyer et al., 2017; Young and Lawrence, 1994). Similarly, the alternans pattern may vary strongly, with some studies reporting that the morning peak was larger than the afternoon peak (Hoy et al., 2012; Hyun and Ellis, 2002, 2000), while others report that pigs had only one peak in feeding activity, either in the morning (Augspurger et al., 2002; Hyun and Ellis, 2001) or in the afternoon (Baumung et al., 2006; Fraser et al., 1991), or that there was a high feeding activity throughout the day (Weiler et al., 2013). Studies that looked at the feeding patterns of individual pigs noted that although many pigs show an alternans feeding pattern, others may eat throughout the day (Gertheiss et al., 2015), may show no consistent pattern across days (Carcò et al., 2018; Hyun et al., 1997; Maselyne et al., 2018; Toft and Madsen, 1998), or may even mainly feed at night (Ingram et al., 1980).

It is likely that part of this variation can be explained by differences in study methodologies, such as the way in which feeding behaviour is measured (*e.g.* using electronic feeding stations, RFID antennas at feeding troughs, or scan sampling from video footage) and processed (*e.g.* including or excluding non-nutritive visits), or in which time frame it is expressed (*e.g.* hourly, daily, or averaged across the growing period or in smaller periods). Beyond that it is, however, known that characteristics of individual pigs and environmental circumstances explain part of the variation, such as sex and castration (*e.g.* Fàbrega et al., 2010; Guo et al., 2015a; Schmidt et al., 2011), breed (*e.g.* Augspurger et al., 2002; Fernández et al., 2011; Renaudeau et al., 2006, 2005), genetics (*e.g.* Ding et al., 2017; Do et al., 2013b; Guo et al., 2015b), body weight and growth rate (*e.g.* Brown-Brandl et al., 2013; Gonyou and Lou, 2000; Turner et al., 2002), personality (*e.g.* Boumans et al., 2018a; Rohrer et al., 2013), feed content (*e.g.* Castilha et al., 2016; Quemeneur et al., 2019; Whittemore et al., 2001a; Zeng et al., 2019), the use of dry or wet feed (*e.g.* Bergstrom et al., 2012; Botermans and Svendsen, 2000; Gonyou and Lou, 2000), the type and location of the feeder (*e.g.* Botermans et al., 2000; Botermans and Svendsen, 2000; Nielsen et al., 1996a), lighting regime (*e.g.* Feddes et al., 1989; Ingram et al., 1980), season (*e.g.* Mensching et al., 2018; Schulze et al., 2001; Xin et al., 2016), management procedures such as weighing (*e.g.* Augspurger and Ellis, 2002), and the lasting effects of the environment and condition of the mother during gestation (*e.g.* Sell-Kubiak et al., 2013). In addition, some of the variation may be due to the differences in pig welfare states. For example, clinically diseased pigs will show a lower feed intake than healthy pigs (*e.g.* Brown-Brandl et al., 2013; Helm et al., 2018a, 2018b; Munsterhjelm et al., 2015; Schweer et al., 2016), and pigs subjected to severe feed competition will show lower feeding frequencies and higher intakes per visit than pigs housed in non-competitive situations (*e.g.* Georgsson and Svendsen, 2002; Labroue et al., 1999; Morrow and Walker, 1994a; Nielsen et al., 1995; Wallenbeck and Keeling, 2013). In the next section, we describe these relationships between feeding patterns and pig welfare in detail, using a systematic literature review.

4. Feeding patterns and pig welfare

4.1. Clinical disease

On the relation between feeding patterns and clinical disease, 18 papers were identified. A summary of the main findings is provided in Table 1.

Across animal species, clinical disease induces a drop in daily feed intake, called anorexia, as part of the sickness response (reviewed by Johnson, 2002). In pigs, several studies have reported such an intake drop, for example during pneumonia (Brown-Brandl et al., 2013), lameness (Munsterhjelm et al., 2015), bacterial infection (Helm et al., 2018a, 2018b), and viral infection (Schweer et al., 2016), although one study reported no reduction in feed intake during mild viral infection (Er et al., 2014). Deviations in daily feed intake have been used to effectively identify more and less disease resilient pigs, where the authors defined disease resilience as the ability to maintain relatively undiminished performance during infection (*i.e.* pigs more affected by disease would show larger reductions in feed intake) (Putz et al., 2019). Nevertheless, as clinical disease was not monitored, in the study of Putz et al. (2019) it cannot be reliably concluded that pigs with deviating feeding patterns were indeed less resilient to disease, although at group level resilience was seen to correlate with veterinary treatments and mortality. Feed intake reduction may occur long before clinical signs are evident, such as up to twenty days before diagnosis of lameness (Munsterhjelm et al., 2015), but in the case of infection it usually occurs after initial infection (Sandberg et al., 2006). The severity of the intake reduction can be highly variable. Munsterhjelm et al. (2015) reported that the extent of the daily feed intake reduction in response to lameness depended on pig age, with younger pigs being more affected, and differed between pigs that would or would not recover (25.5–45.6 % *vs.* 55.3–99.2 % reduction in intake). There are also some indications that intake reduction depends on sex and genetic line (Frank et al., 2005), and it has been theorised that onset, severity, and recovery differ between diseases (Munsterhjelm et al., 2015), pathogen types (Ahmed et al., 2014) and pathogen load during initial infection (Frank et al., 2005). It is generally assumed that pigs do not compensate for reduced intake by increasing intake post-recovery (Pastorelli et al., 2012), however, there is no empirical evidence supporting or refuting this assumption. One study has reported that feed intake increased after antibiotic administration (Hauschild et al., 2020), but as the reason for administration was not reported, no conclusion regarding compensatory feeding can be drawn from this finding.

Although the impact of clinical disease on feed intake is quite clear, there is less knowledge on its impact on the behaviours that underlie intake. Several studies have reported that daily feeding duration severely reduces during clinical disease (Adrion et al., 2018; Ahmed et al., 2014; Kapun et al., 2016; Putz et al., 2019), leading Brown-Brandl et al. (2016) to use modelling techniques to detect reductions in feeding duration to identify pigs suffering from pneumonia. With their model, they were indeed able to detect all 5 sick pigs and 17 out of their 21 sick days, but as these pigs were initially identified as suffering from pneumonia by their large drop in feed intake, not from clinical signs, they represent only unconfirmed cases. In addition, it is likely that only severe cases were detected here, as less severe cases could be theorised to

Table 1
The effect of clinical disease on feeding patterns (intake (*inta*), duration (*dur*), frequency (*freq*) & rate) compared to feeding patterns of healthy pigs (increase ↑, decrease ↓, or no difference ≈). Empty cells show that no papers were found on this topic. The final column indicates the number of papers that support or contradict this finding. *An overview of the papers this table is based on can be found in Supplementary Table* 1.

Clinical disease	Daily level			Meal level			Visit level			Reference count	
	Inta	*Dur*	*Rate*	*Inta*	*Dur*	*Freq*	*Inta*	*Dur*	*Freq*	*Support*	*Contrast*
Coughing		↓								1[a]	0
Diarrhoea		≈								1[a]	0
Lameness	↓	↓								2[a]	0
Osteochondrosis	≈		↑					↑	↓	1	0
Pneumonia		↓								4[a]	0
Skin lesions	↓	≈								2[a]	0
Bacterial or viral infection	↓	↓							↓[b]	5	1

Note that studies counted as supporting may support only part of the results in a row, as not all parameters were studied in all counted references, and that the same paper may be counted as both supporting and contrasting when it supports the findings of some feeding parameters but contrasts those of others. Some papers included in the review were not included in this table due to incompatible study designs.

[a] One result was not statistically tested.

[b] This result was only seen in the morning.

show smaller drops in feed intake. The extent to which feeding duration reduces during clinical disease may be highly variable between pigs, even when they are exposed to the same conditions. For example, pigs suffering from pneumonia reduced their daily feeding duration to between 0.33 and 48.33 min per day, maintained this for 1d to 12d, and completely stopped eating during 0d to 4d (Adrion et al., 2018). Moreover, reduced feeding duration may not occur during all types of disease, as it was reported for lame and coughing pigs but not in pigs suffering from diarrhoea or skin lesions (Kapun et al., 2016). This illustrates the necessity of distinguishing between disease types when studying impacts on feeding behaviours. It is currently unclear whether the reduction in daily feeding duration is the result of a reduced feeding frequency or visit duration. One study reported that feeding frequency reduced after bacterial infection, but this was only seen in morning hours (Ahmed et al., 2014). In addition, Munsterhjelm et al. (2017) reported that pigs with clinical osteochondrosis had a lower feeding frequency and higher visit duration than pigs with subclinical osteochondrosis, but when compared to healthy control pigs, clinical osteochondrosis solely led to a tendency for lower feeding frequency. It should be noted, however, that in this study the control group was very small (n = 3) and that a lack of statistical power may have obscured differences between clinically ill and healthy pigs.

The role of other feeding behaviours in relation to clinical disease is currently unknown. Feeding rate was considered in only one study, which reported a lower rate in pigs with clinical compared to subclinical osteochondrosis, but a similar rate between clinically ill pigs and healthy controls although the control group was very small (n = 3, Munsterhjelm et al., 2017). In addition, Kapun et al. (2017) proposed that a drop in the number of pigs eating simultaneously may indicate lameness in the pig that became more solitary, or that lameness may be present in pigs that delay their first morning meal, but these potential indicators have not yet been tested empirically. Other parameters, such as visit interval or the frequency of non-nutritive visits, have, to our knowledge, not been studied in relation to clinical disease.

4.2. Subclinical disease

On the relation between feeding patterns and subclinical disease, 3 papers were identified. A summary of the main findings is provided in Table 2.

Subclinical diseases are diseases that come with few to no clinical signs (*i.e.* they are asymptomatic) and are hence often detected only after slaughter or when they proceed to become clinical. Although there have been few direct studies into the relation between subclinical disease and feeding patterns in pigs, there are some indications that subclinical diseases might alter feeding patterns. Although no studies have related subclinical diseases to daily feed intake, one study showed that pigs kept in low hygienic conditions, which predisposes pig to (sub) clinical disease, had a lower daily feed intake than pigs kept in clean conditions (Renaudeau, 2009). In addition, these authors found that pigs in unhygienic conditions changed some of their underlying feeding behaviours: pigs in unhygienic conditions had a lower feeding rate, meal size and meal duration, but an equal daily feeding duration, feeding frequency and proportion of feed eaten during the day, compared to pigs kept in hygienic conditions. More direct relationships between subclinical disease and the feeding behaviours that underlie daily intake have been reported as well. Maselyne et al. (2018) proposed that some reductions in feeding duration, which could not be associated to clinical disease, might have been due to subclinical disease, as post-mortem data showed that one such pig suffered from internal abscesses. In addition, pigs that were diagnosed with osteochondrosis after a CT scan, but showed no lameness, visited the feeder more often, for a shorter duration and at a higher feeding rate than pigs that did show lameness (Munsterhjelm et al., 2017). Although these studies do not provide conclusive evidence as to how subclinical diseases impact feeding patterns, they do illustrate that relations between feeding patterns and certain subclinical diseases exist.

4.3. Thermal stress

On the relation between feeding patterns and thermal stress, 27 papers were identified. Summaries of the main findings are provided in Table 3.

Thermal stress occurs when ambient temperature is outside a pig's thermoneutral zone. In commercial husbandry, this can occur when outside temperatures are extreme or when climate-control technology malfunctions. As the exact thermoneutral zone differs between studies, depending on for example body weight and air humidity (National Research Council, 2012), studies applying temperatures higher and lower than the thermoneutral zone are accumulated as studies looking at heat and cold stress, respectively.

4.3.1. Heat stress

The effect of heat stress on pig feeding patterns is generally assessed by increasing the temperature above the thermoneutral zone, either constantly or in a cyclic fashion, *i.e.* with higher temperatures during the day than night. Commonly, the impact of the high ambient temperature on the pigs is not further assessed, as only few studies have included measurements on body temperature (Lopez et al., 1991a; Morales et al., 2018) or behavioural signs of heat stress, such as panting (Lopez et al., 1991a). Nevertheless, all studies have reported that pigs reduce their feed intake during putative heat stress (Brown-Brandl et al., 2000; Collin et al., 2001; dos Santos et al., 2018; Hyun et al., 1998b; Lopez et al., 1991a; Nienaber et al., 1987; Quiniou et al., 2000b, 2000a; Renaudeau et al., 2006; Rinaldo et al., 2000; Xin and DeShazer, 1992). This is an adaptive response, as feed intake during heat stress further increases body temperature, especially when intake occurs in the evening (Cervantes et al., 2018). When ambient temperature returns to the thermoneutral zone (Kerr et al., 2005) or pigs are sprayed with water (Eigenberg et al., 2002), feed intake increases rapidly to levels similar to or temporarily exceeding normal. When high temperatures persist, pigs will over time increase their feed intake levels back to baseline (dos Santos et al., 2018; Lopez et al., 1991a). The severity of the reduction in feed intake depends on pig factors, including breed (Cross et al., 2020;

Table 2
The effect of subclinical disease on feeding patterns (intake (*inta*), duration (*dur*), frequency (*freq*) & rate) compared to feeding patterns of healthy pigs (increase ↑, decrease ↓, or no effect ≈). Empty cells show that no papers were found on this topic. The final column indicates the number of papers that support or contradict this finding. *An overview of the papers this table is based on can be found in Supplementary Table* 2.

Subclinical disease	Daily level			Meal level			Visit level			Reference count	
	Inta	*Dur*	*Rate*	*Inta*	*Dur*	*Freq*	*Inta*	*Dur*	*Freq*	*Support*	*Contrast*
Low hygiene level	↓	≈	↓	↓	↓	≈			≈	1	0
Internal abscesses		↓								1[a]	0
Osteochondrosis			↓					↓	↑	1	0

Note that studies counted as supporting may support only part of the results in a row, as not all parameters were studied in all counted references, and that the same paper may be counted as both supporting and contrasting when it supports the findings of some feeding parameters but contrasts those of others.
[a] This result was not statistically tested, and is theorised from the findings of one pig only.

Table 3
The effect of high and low ambient temperatures on feeding patterns (intake (*inta*), duration (*dur*), frequency (*freq*) & rate) compared to feeding patterns of pigs at control conditions (treatment *vs.* control, increase ↑, decrease ↓, or no effect ≈). Empty cells show that no papers were found on this topic. In case of ties for the main effect, papers with animal-based parameters were given greater weight than those with resource-based parameters, and if this was insufficient both results are shown. The final column indicates the number of papers that support or contradict the main finding. *An overview of the papers this table is based on can be found in Supplementary Table* 3.

Thermal stress	Daily level			Meal level			Visit level			Reference count	
	Inta	*Dur*	*Rate*	*Inta*	*Dur*	*Freq*	*Inta*	*Dur*	*Freq*	*Support*	*Contrast*
Constant hot (±30 °C) *vs.* thermoneutral	↓	↓	↑≈	↓	↓	≈			↑	6	2
Hot day *vs.* thermoneutral	↓		≈	≈		≈				3	0
Hot day & less hot night *vs.* constant hot	≈		≈							1	0
Large *vs.* small heat variation between day and night	↓			≈	≈	↓				2	0
Hot season or hot outside temperature *vs.* thermoneutral	↓[a]	↓[b]	≈	↓	↓	↑			≈	4	3
Constant cold (1–13 °C) *vs.* thermoneutral	↑	↑	↓	↓	↓≈				↑	5	0
Cold night & thermoneutral day *vs.* hot day & thermoneutral night	↑	↑	≈	≈		≈				1	0

Note that studies counted as supporting may support only part of the results in a row, as not all parameters were studied in all counted references, and that the same paper may be counted as both supporting and contrasting when it supports the findings of some feeding parameters but contrasts those of others. Some papers included in the review were not included in this table due to incompatible study designs.

[a] In one study, the results depended on age: ↑ from 15 to 30 kg, ↓ from 35 to 90 kg & overall from 15 to 90 kg.

[b] In one study, the results depended on breed: ↑ for Yorkshire- and Duroc-sired pigs, ↓ for Landrace-sired pigs.

Wellock et al., 2003) and age (Nienaber et al., 1996; Quiniou et al., 2000a; Rinaldo et al., 2000), and environmental factors, including group size (Kerr et al., 2005) and feeding regime (dos Santos et al., 2018). More specifically: older and hence larger pigs are more affected by high temperatures than younger and hence smaller pigs; individually-housed pigs are more affected than group-housed pigs, but group-housed pigs become more affected as pig densities increase; and precision feeding (*i. e.* where the exact ration is calculated for each pig individually) may reduce the impact of high temperatures because the optimised nutrient composition allows for a lower feed intake and hence less heat production during digestion. In addition to reducing feed intake, pigs may shift their feeding (peaks) earlier into the morning and later into the night (Cross, 2017; Cross et al., 2020; dos Santos et al., 2018; Feddes et al., 1989; Ingram et al., 1980; Quiniou et al., 2000a, 2000b; Renaudeau et al., 2006; Xin and DeShazer, 1992), but not if the high temperature persists during the night (Collin et al., 2001).

How these changes in feed intake are mediated by underlying feeding behaviours is not fully clear. There is general agreement that daily feeding duration declines as temperatures rise (Brown-Brandl et al., 2000; Collin et al., 2001; Fraga et al., 2019; Gertheiss et al., 2015). Although one study reported no such reduction (Renaudeau et al., 2006), in this observational study the difference in ambient temperature between the warm and hot season was relatively small and may hence have been insufficient to induce differences. Cross et al. (2018) determined that the extent of the reduction in feeding duration in response to heat stress is heritable, as it appears mediated by DNA sequences that code for proteins involved in for example immune function, the endocrine system and vasoconstriction. Lower daily feeding duration and intake may be due to reduced feeding frequency (Brown-Brandl et al., 2000; Cross et al., 2020; Xin and DeShazer, 1992), feed intake per meal (Brown-Brandl et al., 2000; dos Santos et al., 2018) and meal duration (Brown-Brandl et al., 2000; Nienaber et al., 1996; Renaudeau et al., 2006), but many studies also reported no impact of heat stress on these parameters (Collin et al., 2001; Nienaber et al., 1996; Quiniou et al., 2000a; Renaudeau et al., 2006; Xin and DeShazer, 1992). Feeding rate has been reported to be higher (Brown-Brandl et al., 2000; Nienaber et al., 1996), lower (dos Santos et al., 2018) or unchanged (Collin et al., 2001; Feddes et al., 1989; Quiniou et al., 2000a; Renaudeau et al., 2006) during high temperatures. The wide range of reported impacts of high temperatures on feeding behaviours is likely a consequence of the wide range of treatments, animals and housing conditions used. Treatments have consisted of cyclic or constant temperatures, with maximum temperatures ranging from 25 to 40 °C, or studies have simply followed outside temperatures. Pig breeds used ranged from high-productive breeds such as Piétrain and Large White to heat-resistant breeds such as the Creole, or crosses of different breeds. Housing conditions ranged from individual to group housing, and different diets and lighting regimes were used. It is hence conceivable that although the impacts of heat stress on feed intake and duration are similar across circumstances, they result from divergent adaptations in the underlying feeding behaviours. These adaptions depend on, among others, pigs' physical abilities, their housing circumstances and the exact nature of the high ambient temperatures.

4.3.2. *Cold stress*

Low ambient temperatures, in contrast to high ones, prompt pigs to increase their feed intake. The increased feed intake is required to maintain body temperature (Gertheiss et al., 2015; Lopez et al., 1991b; Nienaber et al., 1990; Quiniou et al., 2000a; Whittemore et al., 2001b) and not for growth, as pigs show reduced growth during cold stress (Lopez et al., 1991b; Nienaber et al., 1987). Unlike heat stress, cold stress does not induce pigs to eat at different day times than preferred (Quiniou et al., 2000a). If cold stress persists, feed intake will reduce back to baseline levels after about two weeks (Lopez et al., 1991b). The extent to which feed intake increases depends, among others, on pig body size and feed composition. Specifically, small pigs increase their intake more than large pigs, indicating a higher susceptibility to cold stress (Quiniou et al., 2000a). The extent to which intake can be increased appears constrained by gut capacity and feed type, as pigs fed on feed rich in fibres did not show this typical increase in intake (Whittemore et al., 2001b). It might, therefore, be that small pigs simply cannot increase their intake as much as large pigs due to limitations in gut capacity.

Only a few studies have looked at the impact of cold on the feeding behaviours underlying intake, and their results are quite consistent. Higher feed intake coincides with a longer daily feeding duration (Gertheiss et al., 2015; Nienaber et al., 1990; Quiniou et al., 2000a), due to a lower feeding rate (Nienaber et al., 1991, 1990), a higher feeding frequency (Nienaber et al., 1991, 1990), and a lower visit interval (Nienaber et al., 1991). Meanwhile, feed intake and feeding duration per visit are reduced (Nienaber et al., 1991) or not affected (Quiniou et al., 2000a). Although these consistent results would suggest that the impact of cold stress on pig feeding behaviour is more consistent than that of heat stress, the number and diversity of studies on which this is based is much smaller for cold than for heat stress and does hence not allow such a firm conclusion. Expanding the range of animals and cold treatments used might reveal situation-specific adaptations to cold stress similar to those seen during heat stress.

4.4. Social behaviour

Pigs are a highly social species that naturally live in family groups and show elaborate social interactions (D'Eath and Turner, 2009). Although housing with conspecifics is essential for the expression of natural social behaviour, group housing also has an extensive impact on pig feeding patterns. Several modelling studies have addressed the importance of social interactions for feeding patterns (Boumans et al., 2018a, 2018b; Wellock et al., 2003). Genomic studies that modelled feeding behaviour have repeatedly shown that indirect genetic effects, which largely reflect the social interactions between pen mates, contribute strongly to the variation in feeding behaviours between pigs (Do et al., 2013a; Herrera-Cáceres et al., 2019; Lu et al., 2017; Ragab et al., 2019). This becomes even more pronounced when the indirect genetic effects are calculated based on between-pig differences in feeding behaviours, to reflect that not all dyads of pigs have the same level of interaction (*i.e.* pigs that have widely different feeding patterns are assumed to have a lower level of social interaction than pigs that had similar feeding patterns) (Ragab et al., 2019). In addition, remarkable differences in feeding patterns have been reported between pigs housed individually and pigs housed in groups, where group-housed pigs could have either one individual feeder or sufficient feeder spaces to accommodate all pigs simultaneously. Group-housed pigs show either a similar (de Haer and de Vries, 1993) or a lower (de Haer et al., 1992; Gonyou et al., 1992; Kerr et al., 2005; Nielsen et al., 1996b) feed intake than pigs housed individually, despite a higher intake per visit and meal (Bornett et al., 2000; de Haer and de Vries, 1993). These differences mainly result from a lower feeding frequency in group-housed than individually-housed pigs (Bornett et al., 2000; de Haer et al., 1992; de Haer and de Vries, 1993; Nielsen et al., 1996b), which is partly compensated by a higher visit or meal duration (Bornett et al., 2000; de Haer and de Vries, 1993) and a higher feeding rate (Bornett et al., 2000; de Haer et al., 1992; de Haer and de Vries, 1993). Group housing supports pigs' diurnal, alternans feeding pattern, even when external Zeitgebers are eliminated (Ingram et al., 1980). Currently, there are three theories as to how group housing influences feeding patterns (Bornett et al., 2000; Nielsen, 1999). The first theory claims that pigs adapt their feeding patterns in response to competition for access to the feed. The second builds on the first, by suggesting that social facilitation (*i.e.* observing another pig feeding induces a pig to start feeding itself) enhances feed competition and hence further alters feeding patterns. The third theory suggests that it is the individually- rather than the group-housed pigs that show deviant feeding behaviour, as a lack of stimuli induces them to visit the feeder more often. To our knowledge, no attempts have yet been made to interpret empirical study results in light of the third theory. Below, we will discuss the evidence that underlies the first two theories. In total, 58 papers were identified. A summary of the main findings is provided in Table 4.

4.4.1. Feed competition

Feed competition has been extensively studied in growing-finishing pigs, due to its relationship with growth and carcass quality (*i.e.* lesioning). It mostly consists of one pig displacing another from the (individual) feeder, either with or without aggressive behaviours such as biting, and can in some cases lead to fights. Studies on feed competition generally focus on either resource- or animal-based parameters related to competition. More specifically, studies either manipulate the physical or social environment to influence competition, *e.g.* by changing feeder space or grouping pigs in high or low weight-diverse groups, or look at the feeding patterns of pigs with different characteristics, such as dominance ranks.

4.4.1.1. Adaptations to resource-induced feed competition at pen level. Feed competition can be manipulated using a wide range of resource changes, including space allowance, group size, feeder space, feeder location, and how similarly sized the pigs in one pen are. In addition, mixing pigs into new groups may temporarily increase feed competition, until a new dominance order has been established. In general, competition becomes worse when pen and feeder space decrease, group size increases, feeders are placed closer together, and when pigs become more similar in body weight, as pigs of similar weight have more trouble establishing a clear dominance order (Andersen et al., 2000). The effect of these competition-influencing factors on feeding patterns has often been studied in co-occurrence (*e.g.* group size was increased but the number of feeders remained the same, confounding larger group size with lower feeder allowance), making it difficult to pinpoint how each factor independently influences feeding patterns. When the factors could be split, they indicated similar effects on feeding patterns. Therefore, we accumulated these factors as leading to high or low feed competition, and present them as combined results (an overview of the split results can be found in Supplementary Table 4).

In general, it has been reported that feed competition will induce

Table 4
The effect of resource- and animal-based manipulations of social behaviour on pig feeding patterns (intake (*inta*), duration (*dur*), frequency (*freq*) & rate) (treatment *vs.* control, increase ↑, decrease ↓, or no effect ≈). Empty cells show that no papers were found on this topic. In case of ties for the main effect, papers with animal-based parameters were given greater weight than those with resource-based parameters, and if this was insufficient both results are shown. The final column indicates the number of papers that support or contradict the main finding. *An overview of the papers this table is based on can be found in Supplementary Table* 4.

Social behaviour	Daily level			Meal level			Visit level			Reference count	
	Inta	*Dur*	*Rate*	*Inta*	*Dur*	*Freq*	*Inta*	*Dur*	*Freq*	*Support*	*Contrast*
Group *vs.* individual housing	↓	↓≈	↑	↑	↑		↑		↓	8	3
More animals per feeder	≈	↓	↑				↑	↑↓	↓	12	8
Less trough space per pig	↓	↓						≈	≈	2	0
Feeders closer together	≈								↓	1	0
Absence *vs.* presence of protective crate	≈							↓	↑	1	0
More pigs per pen	≈	↓	↑	↓≈	↑↓	↑↓	↑↓	≈	↓	7[a,b]	3
Mixing *vs.* no mixing	≈↓	≈	≈					↑	↓	2	0
Lower space allowance	≈↓	≈	≈				↑	↑↓≈	↓	8[c]	3
Dominant *vs.* subordinate (*classification methods accumulated*)	≈	↑	↑↓≈	↑	≈	≈	↑	↑↓	↑↓≈	11	4
Large *vs.* small body size	↑	↓	↑≈		≈		↑		↓	3[d]	1

Note that studies counted as supporting may support only part of the results in a row, as not all parameters were studied in all counted references, and that the same paper may be counted as both supporting and contrasting when it supports the findings of some feeding parameters but contrasts those of others. Some papers included in the review were not included in this table due to incompatible study designs.

[a] The effect of group size on feed intake per visit was inconsistent, with groups of 12 pigs having a lower intake per visit than groups of 8 pigs, while groups of 4 pigs had a lower intake per visit than groups of 12 or 8 pigs.

[b] The effect of group size on feed intake per meal, meal duration and meal frequency differed between breeds.

[c] The effect of lower space allowance on visit duration depended on age.

[d] Medium-sized pigs showed a higher feeding rate than small or large pigs.

pigs to maintain daily feed intake by changing their underlying feeding pattern (Edwards et al., 1988; Gonyou and Lou, 2000; Hansen et al., 1982; Hyun et al., 1998a; Hyun and Ellis, 2002; McGlone and Newby, 1994; Mikesell and Kephart, 1999; Morrison et al., 2003; Nielsen et al., 1995; O'Connell et al., 2004; Pearce and Paterson, 1993; Rasmussen et al., 2006b; Schmolke et al., 2003; Spoolder et al., 1999; Tindsley and Lean, 1984; Wiegand et al., 1994). When these adaptations are insufficient, feed intake reduces (Edmonds et al., 1998; Georgsson and Svendsen, 2001; Hyun et al., 1998a, 1998b; Hyun and Ellis, 2001; McGlone and Newby, 1994; Morrow and Walker, 1994a; Turner et al., 2002; Walker, 1991). At pen level, pigs will reduce their daily feeding duration during competition (Botermans and Svendsen, 2000; Georgsson and Svendsen, 2002; Gonyou and Lou, 2000; Hyun et al., 1998a; Hyun and Ellis, 2001; Labroue et al., 1999; Morrow and Walker, 1994a; Nielsen et al., 1995; Turner et al., 2002), and hence maintain their daily feed intake levels by increasing feeding rate (Botermans and Svendsen, 2000; Hyun and Ellis, 2002, 2001; Labroue et al., 1999; Nielsen et al., 1995; Rasmussen et al., 2006a). A few studies, however, reported no effect of group size or space allowance on feeding duration (Hyun et al., 1998a; Hyun and Ellis, 2002; Pearce and Paterson, 1993; Spoolder et al., 1999) or rate (Hyun et al., 1998a), implying that feeder space is likely to be the more determining factor. The changes in daily feeding duration and rate are mediated by changes in the frequency and size of the visits and meals. Most studies have reported that, during competition, pigs reduce their feeding frequency (Georgsson and Svendsen, 2002; Hansen et al., 1982; Hyun et al., 1998a; Hyun and Ellis, 2002, 2001; Labroue et al., 1999; Morrison et al., 2003; Morrow and Walker, 1994a; Nielsen et al., 1995; Wallenbeck and Keeling, 2013) and increase their intake (Georgsson and Svendsen, 2002; Hyun et al., 1998a; Hyun and Ellis, 2002; Nielsen et al., 1995) and duration (Hyun et al., 1998a; Hyun and Ellis, 2002; Nielsen et al., 1995) per visit. Several studies have, however, reported no differences (Gonyou and Lou, 2000; Labroue et al., 1999; Morrison et al., 2003; Rasmussen et al., 2006b; Turner et al., 2002; Walker, 1991), or even an increase in feeding frequency (Labroue et al., 1999) and reduction in intake (Hyun and Ellis, 2001; Labroue et al., 1999) and duration (Hyun and Ellis, 2001; Labroue et al., 1999; Rasmussen et al., 2006b; Walker, 1991) per meal. It is likely that these contrasting results are due to the specific study circumstances. For example, the lack of changes in response to competition were likely because Labroue et al. (1999) used a different breed than all other studies, and expressed feeding behaviour at meal rather than visit level. The deviating results of Turner et al. (2002) and Rasmussen et al. (2006b) were likely due to them using a trough rather than single-space feeders, allowing multiple pigs to feed simultaneously. It has been theorised that the exact pattern shown depends on how easily pigs can be displaced from the feeder. If displacement is difficult, such as when a protective crate is used (Morrow and Walker, 1994b), pigs are forced to withdraw from the feeder less often but may have more difficulty in accessing the feeder, leading to a low feeding frequency and high feeding duration per visit during competition. If displacement is easy, pigs, especially small ones (Botermans et al., 2000), are forced to withdraw often and will hence maintain their intake by visiting the feeder often but for small visits each time. This theory corresponds to the results found in a modelling study by Boumans et al. (2018b), in which the simulated pigs could be easily displaced, and from which the authors concluded that a low meal size and duration and a high meal frequency indicate a competitive environment with high displacement levels. It hence appears that the exact environmental circumstances as well as pigs' physical characteristics strongly influence how pigs adapt their feeding patterns to competition.

Besides the behaviours underlying feed intake, several other feeding parameters change in competitive situations and could hence potentially be used as indicators of pig welfare. Diurnal patterns in feeding become less pronounced during competition: as feeder occupation increases (Hyun and Ellis, 2002, 2001; Morrison et al., 2003; Nielsen et al., 1995; Walker, 1991), pigs will eat throughout the day rather than in two distinct peaks (Botermans and Svendsen, 2000; Hyun and Ellis, 2002; Nielsen et al., 1995; Walker, 1991) and will shift part of their feeding behaviour into the night (Botermans and Svendsen, 2000; Georgsson and Svendsen, 2002; Hyun and Ellis, 2002, 2001; Morrison et al., 2003; Morrow and Walker, 1994a; Nielsen et al., 1995; Turner et al., 2002; Walker, 1991). One study saw no effect on diurnal patterns (Simonsen, 1990), but this study had only one group of pigs per treatment and hence likely suffered from insufficient statistical power. Besides night feeding, high feeder occupation also leads to an increase in queuing for access to the feeder (Morrow and Walker, 1994a; Rasmussen et al., 2006a, 2006b; Spoolder et al., 1999; Walker, 1991), albeit not when a trough was used (Turner et al., 2002). Finally, one study reported that, at pen level, the frequency of non-nutritive visits was not affected by competition (Nielsen et al., 1995).

4.4.1.2. Animal-based adaptations to feed competition. Although the previously described changes in feeding patterns due to different levels of feed competition occur on average, at the individual level pigs may show vastly different adaptations, especially when competition becomes more severe (Chen et al., 2010; Walker, 1991). These differences in adaptation strategy are largely due to differences in dominance rank, which in turn is influenced by a range of pig characteristics, such as breed, body weight, sex, and personality (Beilharz and Cox, 1967; Boumans et al., 2018a). Pigs may eat according to rank order only if competition is present, eating randomly when competition is absent (Hansen et al., 1982). Dominance orders can be determined in many ways, such as by using agonistic interactions around the feeder (Hoy et al., 2012) or after mixing (Leiber-Schotte, 2009; Parois et al., 2017), or by extrapolating feeding strategies from correlations between different feeding behaviours (Herrera-Cáceres et al., 2019; Ragab et al., 2019). Besides using dominance orders, many studies have also classified pigs as dominant, intermediate or subordinate, using assumptions based on body weight and gender: large pigs are thought to be more dominant than small pigs (Botermans and Svendsen, 2000; Georgsson and Svendsen, 2002; Rasmussen et al., 2006b), and boars are thought to be most dominant, followed by barrows and finally gilts (Puppe et al., 1991). All these methods have been applied to compare the feeding patterns between pigs of different ranks. Whether different methods result in the same dominance order is currently unclear, but could be questioned as, for example, agonistic interactions around the feeder may be partly driven by feeding motivation, unlike those after mixing.

The differences in feed intake between pigs of different ranks are inconsistent. When dominance order was inferred from pig body size, feed intake was reported to be higher in dominant pigs than in subordinate pigs (Chen et al., 2010; Georgsson and Svendsen, 2002). However, when agonistic interactions were used to determine order, a lower feed intake in dominant pigs was observed (Hoy et al., 2012; Leiber-Schotte, 2009), or no difference (Nielsen et al., 1995). Therefore, it seems likely that the higher feed intake is related to higher nutritional requirements of larger pigs, and not dominance rank per se. Nevertheless, it has been reported that dominant pigs increase their feed intake when competition becomes more severe (Georgsson and Svendsen, 2002), implying that, during competition, high-ranked pigs may dominate the feeder more than nutritionally required.

These changes in feed intake are underlain by large differences in the feeding patterns between dominant and subordinate pigs. Dominant pigs show a feeding behaviour referred to as 'meal eating', while subordinate pigs perform 'nibbling'. More specifically, dominant pigs show a lower feeding frequency than subordinate pigs (Gonyou and Lou, 2000; Hoy et al., 2012; Ragab et al., 2019; Schamun and Hoy, 2011), combined with a higher intake (Boumans et al., 2018a; Georgsson and Svendsen, 2002; Hoy et al., 2012) and duration (Herrera-Cáceres et al., 2019; Hoy et al., 2012; Puppe et al., 1991; Ragab et al., 2019; Schamun and Hoy, 2011; Schönfelder, 2005) per visit or meal. These effects are likely due to subordinate pigs being the victim of forced withdrawals more often than dominant pigs (Botermans and Svendsen, 2000). Indeed, dominant pigs appear to gain access to the feeder more easily, as they have a shorter waiting time than subordinate pigs (Rasmussen et al., 2006b), can feed more frequently during peak hours (Hoy et al., 2012) and show a higher frequency of non-nutritive visits than subordinate pigs despite a lower daily feeding frequency (Georgsson and Svendsen, 2002). Contrasting results were reported by Leiber-Schotte (2009), who found that dominant pigs had a lower feeding duration per day and visit than subordinate pigs but there was no difference in feeding frequency, Nielsen et al. (1995), who found no correlations between dominance rank and any feeding behaviours, and Herrera-Cáceres et al. (2019), who found that dominant pigs had more feeder visits than subordinate. These contrasts may have been due to the different feeder types and methods used to determine the dominance order. Leiber-Schotte (2009) was the only one with a feeder with a full protective crate. In addition, Leiber-Schotte (2009) used the outcome of fights after initial mixing (*i.e.* wins and losses) and Nielsen et al. (1995) used all agonistic interactions, and were hence the only studies using a scoring method uninfluenced by feeding motivation. Herrera-Cáceres et al. (2019) used phenotypic and genetic correlations to identify behavioural strategies, and solely saw that pigs that occupied the feeder longer and ate at a low rate, which were assumed to be dominant pigs, also had more feeder visits with shorter visit intervals. These correlations combined with indirect genetic effects also suggested that dominant pigs carry genes that induce them to stay longer at the feeder, while simultaneously carrying genes that force their pen mates into a subordinate role (Herrera-Cáceres et al., 2019). Subordinate pigs then have a lower feeding frequency due to difficulty in accessing the feeder (Herrera-Cáceres et al., 2019), or, as was reported in other studies, try to adapt to frequent displacement by increasing feeding frequency, reducing the size of each visit, and shifting their feeding behaviour away from peak hours, *i.e.* into the night (Botermans and Svendsen, 2000; Georgsson and Svendsen, 2002).

Whether pigs also individually adapt by changing their feeding rate is not entirely clear, as the results are contradicting. Although most studies reported a higher feeding rate in subordinate than in dominant pigs (Herrera-Cáceres et al., 2019; Ragab et al., 2019), one study reported a higher feeding rate in dominant pigs (Chen et al., 2010), which was possibly due to subordinate pigs eating at a low feeding rate outside of peak hours (*i.e.* at night). It has also been theorised that adaptation through feeding rate is limited by pigs' physical abilities: in a competition-free testing environment, Gonyou and Lou (2000) saw that large pigs have a higher feeding rate than small pigs. Moreover, Georgsson and Svendsen (2002) proposed that small and large pigs show a similar feeding rate when kept in the same pen because small pigs do not have the oral capacity to increase their feeding rate any further in response to competition. Instead, pigs of intermediate size, which were assumed to have intermediate rank, showed the highest feeding rate, as these were physically capable of increasing their feeding rate in response to competition. Two modelling studies support the effect of body weight in adaptation to competition: Wellock et al. (2003) reported that pigs with high growth potential are more severely impacted by space allowance restrictions than pigs with low growth potential, as they reduced feed intake more severely, and Boumans et al. (2018a) reported that almost all feeding behaviours were influenced by growth capacity. In addition, the latter authors proposed that pig coping style or preferred behavioural strategy to deal with conflict might interact with dominance in determining individual feeding patterns during competition (Boumans et al., 2018b, 2018a), however, this has, to our knowledge, not been empirically assessed.

4.4.2. Social facilitation

It has been theorised that watching other pigs eat will induce feeding behaviour in the observing pig, a theory referred to as social facilitation. As social facilitation would lead to more pigs trying to eat simultaneously, it could enhance feed competition. In individually-housed pigs, social facilitation has been frequently reported. Individually-housed pigs were observed to eat simultaneously with a neighbouring pig more often than could be expected by chance (Gonyou et al., 1992). In addition, individually-housed pigs have a higher feed intake when they are provided with neighbours rather than when kept in social isolation (Hsia and Wood-Gush, 1983), although this does not clarify whether it was the feeding activity of these neighbours that induced the higher intake. In a behavioural test, pigs were reported to have a higher feed intake when the distance between feeders was smaller, despite having to shift to another feeder more often (Thomsen et al., 2009). Interestingly, pigs that were neighboured by a group of pigs on each side of the individual pen showed a similarly enhanced level of simultaneous feeding, but only with one of the two neighbouring groups and only if the feeder in the group pen was immediately adjacent to the feeder in the individual pen (Gonyou et al., 1992). It has been reported that social facilitation can induce feeding behaviour even when a pig is not hungry, as pigs that ate to satiation after fasting were observed to resume feeding when a fasted pig began eating in an adjacent pen (Hsia and Wood-Gush, 1984b). Interestingly, resumed feeding occurred more extensively in dominant than submissive pigs, however, it should be noted that pigs were classified as dominant using competition at the feeder and may hence also have been simply more motivated to feed. Although these studies show that individually-housed pigs, with unlimited access to a feeder, are influenced by social facilitation, these results cannot be extrapolated to group-housed pigs, which are subject to competition for access to the feeder.

Studies in group-housed pigs have shown less consistent results than studies in individually-housed pigs regarding the occurrence of social facilitation. Gonyou et al. (1992) reported that group-housed pigs fed from a two-hole feeder ate simultaneously less often than could be expected by chance, suggesting that observing another pig feed actually deterred pigs from feeding, for example due to competition. These results, however, could also be explained by a preference for a certain feeding space of the two-hole feeder and a willingness to wait for its availability, rather than avoidance of simultaneous feeding per se. Regarding feed intake, pigs kept in a group, but provided with only one feeding space, showed higher intake levels than pigs housed in social isolation, but similar to those of pigs housed individually with neighbours (Hsia and Wood-Gush, 1983). When the feeder space was increased by provision of a long feeding trough, feed intake increased again. These results suggest that social facilitation indeed increases feed intake, but that the extent of this increase is limited by feed competition. Alternatively, the pigs kept in social isolation may have had a reduced intake due to a lack of stimulation. With these contrasting results, it could be questioned whether social facilitation is an important contributor to the feeding behaviour of group-housed pigs. Indeed, a recent modelling study concluded that social facilitation only has a minor impact on pig feeding patterns, as adding social facilitation to the model had little effect on the simulated feeding behaviours (Boumans et al., 2018b).

4.5. Tail biting

The most well-known abnormal behaviour in commercial pigs is tail biting. During tail biting, pigs nibble or bite the tail of a pen mate. This, in its severest form, causes wounds or even loss of the victim's tail. In the biter, the behaviour is thought to be indicative of inadequate coping with the environment, and hence the performance of tail biting is, in itself, interpreted as reduced welfare. No papers could be identified that looked at the feeding patterns of biters, but a few papers have reported the feeding patterns of tail-biting victims. Generally, a tail-biting victim is defined as a pig with a fresh tail wound, and the onset of a tail biting outbreak is defined as the moment at which at least one pig in the pen shows a fresh tail wound. In total, 4 papers were identified. A summary of the main findings is provided in Table 5.

At pen level, pigs in pens with at least one tail biting victim showed a

Table 5
The effect of tail wounds on feeding patterns (intake (*inta*), duration (*dur*), frequency (*freq*) & rate) compared to feeding patterns of pigs with intact tails (increase ↑, decrease ↓, or no effect ≈). Empty cells show that no papers were found on this topic. The final column indicates the number of papers that support or contradict the main finding. *An overview of the papers this table is based on can be found in Supplementary Table* 5.

Tail wounds	Daily level			Meal level			Visit level			Reference count	
	Inta	*Dur*	*Rate*	*Inta*	*Dur*	*Freq*	*Inta*	*Dur*	*Freq*	*Support*	*Contrast*
Tail wounds (pen level)	↓									1	0
Tail wounds (individual level)	↓								↓↑	1[a]	0

Some papers included in the review were not included in this table due to incompatible study designs.
[a] Effects depended on age.

lower feeding frequency 6–9wks before outbreak onset (Wallenbeck and Keeling, 2013) and on the day the first tail wound was observed (Viitasaari et al., 2015). Within outbreak pens, however, the victim was reported to have a higher feeding frequency 2–5wks before outbreak onset compared to non-bitten pen mates or pigs in pens with no tail biting (Wallenbeck and Keeling, 2013). During the last few weeks before outbreak onset, pigs in tail-biting pens had a lower feed intake than pigs in control pens (Munsterhjelm et al., 2015; Wallenbeck and Keeling, 2013). The severity of this reduction is lower than the reduction seen in lame pigs and has a faster recovery (Munsterhjelm et al., 2015) but, nevertheless, reduced intake can persist for up to two weeks after outbreak onset (Wallenbeck and Keeling, 2013). The severity of intake reduction was reported to be larger in younger pigs and in pigs that do not recover (Munsterhjelm et al., 2015). Although the reduction in feed intake and feeding frequency once a tail wound has emerged can likely be related to pain and stress, it could be questioned whether the changes in feeding behaviours prior to outbreak onset were the result of early stages of tail biting and social stress, which had yet gone unnoticed, or whether these behaviours rather predisposed pigs to tail biting. For example, pigs with a higher feeding frequency may have to queue for the feeder more often, making them an easy target for tail biting (Wallenbeck and Keeling, 2013). Indeed, when pigs were given a social rank based on their feeding frequency and feed intake per visit (*i.e.* low-ranked pigs were assumed to have a high feeding frequency and a low intake per visit), it was seen that low-ranked pigs had more tail lesions at the beginning of the growing period than high-ranked pigs, but this relationship disappeared before slaughter (Heckmann et al., 2018). These results suggest that pigs with a higher feeding frequency may be more likely to become a victim of tail biting. Regardless of whether the altered feeding behaviour is a cause or result of tail biting, the results imply that tail-biting outbreaks may be detected from a low average feeding frequency at pen level and a reduction in feed intake, while the future victim could possibly be identified from its high feeding frequency.

No studies could be identified that related feeding patterns to other types of abnormal behaviours, such as ear biting, mounting, or belly nosing (Brunberg et al., 2011).

4.6. *Environmental enrichment*

Recent frameworks have expanded the concept of animal welfare from a focus on purely the prevention of negative states (including both physiological and mental states) to the inclusion of positive states (Boissy and Erhard, 2014; Green and Mellor, 2011; Yeates, 2011). How positive states can be identified exactly is still in development, but examples of proposed indicators include cognitive, such as judgement bias, behavioural, such as play or certain vocalisations, and physiological indicators, such as immunological or neurological markers (Yeates and Main, 2008). No studies have yet attempted to relate animal-based indicators of positive states to pig feeding patterns. Nevertheless, several studies have looked at the impact of providing pigs with environmental enrichment, mostly in the form of rooting substrates, on pig feeding patterns, which could be theorised to stimulate positive states. In total, 13 papers were identified. A summary of the main findings is provided in Table 6.

Both straw-based deep litter housing (Morrison et al., 2007) and simple addition of straw to the pen (Bolhuis et al., 2006; Jensen et al., 2019) as environmental enrichment have been reported to increase feed intake. However, in one study this increase was only seen in the morning and disappeared when pigs became older (Fraser et al., 1991), and in another straw availability only increased intake if straw had also been available during the rearing phase (Bolhuis et al., 2006). It might be that straw increases feed intake mostly at a young age, as Peeters et al. (2006) reported that straw does not affect feed intake when provided only during the last six weeks before slaughter. One study reported no difference in feed intake in deep litter-housed pigs (Wei et al., 2019), however, pigs in this study did not have *ad libitum* access to feed and were hence likely limited in increasing their intake by competition and physiological constraints. Although the reported increases in feed intake could be related to more improved welfare, there could be several other explanations. For example, higher intake may be due to physiological changes, such as better gut health (Jensen et al., 2019). Indeed, other forms of environmental enrichment may have very different effects on feeding behaviour. Providing pigs with mushroom compost as enrichment led to a lower rather than a higher feed intake compared to pigs not provided with any enrichment, although intake levels were not lower than in pigs provided with an empty rack (Beattie et al., 2001). In

Table 6
The effect of environmental enrichment on feeding patterns (intake (*inta*), duration (*dur*), frequency (*freq*) & rate) compared to feeding patterns of pigs without enrichment (increase ↑, decrease ↓, or no effect ≈). Empty cells show that no papers were found on this topic. In case of ties for the main effect, papers with animal-based parameters were given greater weight than those with resource-based parameters, and if this was insufficient both results are shown. The final column indicates the number of papers that support or contradict the main finding. *An overview of the papers this table is based on can be found in Supplementary Table* 6.

Environmental enrichment	Daily level			Meal level			Visit level			Reference count	
	Inta	*Dur*	*Rate*	*Inta*	*Dur*	*Freq*	*Inta*	*Dur*	*Freq*	*Support*	*Contrast*
Deep litter housing	↑≈	↑			↑				↓	3	0
Availability of straw	≈	≈	≈				≈	≈	↑≈	5	3
Availability of other rooting material	↓≈	↓								2	0
Rotation of toys		↓								1	0
Group-farrowing with creep feed in early life	↓									1	0

Note that studies counted as supporting may support only part of the results in a row, as not all parameters were studied in all counted references, and that the same paper may be counted as both supporting and contrasting when it supports the findings of some feeding parameters but contrasts those of others.

addition, exposing piglets to group-farrowing during the first 8 weeks of life, which is thought to be better for welfare than confinement-farrowing, decreased feed intake in the first 6 weeks after arriving in the growing-finishing unit (Li et al., 2012).

Very little is known about how the behaviours underlying feed intake are affected by environmental enrichment. One study showed that pigs in deep litter housing at a higher space allowance had a lower feeding frequency and higher meal duration than pigs housed on slatted floors at a lower space allowance (Tallet et al., 2013). Another study, however, reported the opposite pattern, where pigs provided with straw had a higher feeding frequency and a lower intake per visit, leading to a shorter daily feeding duration, than pigs denied straw (Morgan et al., 1998). These authors also reported that pigs provided with straw had a clearer alternans feeding pattern with higher and earlier feeding peaks than pigs without straw. In a follow-up study, however, none of these effects could be reproduced (Morgan et al., 1999), to which the authors concluded that feeding frequency was only higher after pigs switched from no straw to straw, and became lower when pigs were switched from straw to no straw. It is likely that the contrasting results of these studies are due to specific housing circumstances. For example, Morgan et al. (1999, 1998) theorised that the higher feeding frequency was due to the straw rack being closer to the feeder than the resting area, giving pigs with straw a lower cost of feeding than pigs without straw, as they already spent more time close to the feeder. In Tallet et al. (2013), on the other hand, straw was provided throughout the pen, hence no such cost reduction was present. Two more studies reported no effect of straw bedding (Peeters et al., 2006) or wood chip provision (Jensen and Pedersen, 2010) on feeding duration. It should be noted that both of these studies had a very limited observation period (once per week 5 min, or 60 min after feeding) and hence are unlikely to provide a good representation of daily feeding duration. Finally, one study reported a decrease in daily feeding duration when pigs were provided with a rotation of toys (Pearce and Paterson, 1993), but this was only tested under overcrowded conditions.

5. Discussion

The aim of this study was to review the current knowledge on the relationships between feeding patterns and the welfare of growing-finishing pigs. In the literature, numerous links between feeding patterns and pig welfare have been described, implying that data from electronic feeding stations is indeed a promising tool to continuously monitor pig welfare. Deviations from ‘normal’ feeding behaviour may occur swiftly in response to reduced welfare, and may sometimes precede other clinical or behavioural manifestations of reduced welfare, such as for clinical disease and tail biting. These links are particularly established between feed intake and physiological welfare problems, such as clinical health, thermal stress and tail biting wounds. The severity of reduction in intake in response to these physiological problems could even enable distinguishing clinical disease from tail biting, as with clinical disease the reductions seem more severe. The behaviours underlying feed intake provide further information, as they showed distinct deviations for different disease types and may allow early detection of disease at a subclinical stage. Combining feed intake with its underlying behaviours (feeding frequency, duration and rate), therefore, may be more effective in detecting and differentiating reduced welfare states. A better understanding of how these underlying feeding behaviours respond to a wider range of clinical and subclinical diseases is, however, warranted before this knowledge can be utilised as a welfare assessment tool. In addition, it should be noted that the responses of these underlying behaviours may in some cases be too diverse between different housing conditions to be good, generic indicators of welfare. This is the case, for example, with thermal stress, where changes in feeding patterns are strongly dependent on pig characteristics, housing and management. An interesting finding is that, in some cases, there may be additional value in studying the feeding patterns on a shorter time scale, within the day. Currently, most studies have been performed using daily averages, but there are indications that some feeding behaviours may only deviate during parts of the day, often in the morning (Ahmed et al., 2014; Fraser et al., 1991; Kapun et al., 2017). In addition, studies have often been performed at either pen or pig level, while it may be advantageous to combine both pen and pig level observations, such as was reported for tail biting outbreaks (Wallenbeck and Keeling, 2013). These paths warrant further research attention.

On the behavioural side, mostly the feeding behaviours that underlie intake, rather than feed intake itself, deviate from normal during stressful situations. Feed competition appears to have a strong effect on underlying feeding behaviours, but not intake, influencing both the average pattern of the group and the variation in patterns between pigs within a pen. Nevertheless, it could be questioned whether these adaptations should be considered indicative of reduced welfare, as they might be a reasonable coping mechanism with which pigs adapt effectively to their environment. It is currently unclear whether severe social stress induces different feeding patterns that can be distinguished from ‘acceptable’ variation due to effective coping, although it could be theorised that this point is reached when daily feed intake reduces. For abnormal behaviours, the presence of stress is clearer, and as mentioned previously, for tail biting it appears possible to identify tail biting victims based on pig and pen level deviations in feeding patterns. Whether these results extrapolate to other forms of abnormal behaviour, such as ear biting, mounting or belly nosing, is currently unknown. In addition, it is unknown whether biters, in addition to victims, also show deviations in their feeding patterns, which is highly relevant from a practical perspective as it would allow the farmer to identify and remove the biter from the pen rather than its victims.

Although there is currently a large number of studies that consider physiological and behavioural aspects of welfare, the affective part of welfare has been largely overlooked in the context of pig feeding patterns. Although negative affective states, such as pain or frustration, could reasonably be assumed for the different physiological and behavioural welfare problems covered in this review, explicit links between specific affective states and these welfare problems have not yet been made. It is, for example, yet unknown whether other negative affective states, such as depression, are linked to specific feeding patterns, and on the positive side of affect only very little knowledge is available. Although some studies have looked at the effects of environmental enrichment, mostly rooting material, on feeding patterns, their effects are inconsistent. It seems likely that these effects depend on the exact enrichment and environment provided, and hence may not be a good representation of positive affect. Based on knowledge of resilience in animals (Colditz and Hine, 2016), it could be theorised that pigs with positive affective states may have feeding patterns that are stable over time. Animal-based measurements of both positive and negative affective states are required to gain more knowledge on the potential relationships between affective state and pig feeding patterns.

We want to emphasize that many studies have reported a large variation in feeding patterns at least between pigs, but potentially also within pigs over time. This implies that it might be difficult to accurately isolate the variation in feeding patterns that is informative of pig welfare. Therefore, it is important to further understand this variation, especially at the level of the individual pig. It is conceivable that pigs with different basal feeding patterns, for example due to differences in dominance rank, may respond to similar welfare problems in a different way. This finding suggests that a combination of group and individual feeding patterns should be used to monitor pig welfare. Individual feeding stations are ideal to obtain this group and individual feeding pattern data, and additionally create opportunities to combine feeding patterns with other sensors that provide additional information on pig production and welfare. As each pig that enters the feeder will be isolated, individually recognised, and will stand still within the feeder, data could for example be gathered on body weight (with a scale or 3D cameras), body temperature (with thermal imaging or an IR thermometer) or even facial expressions (with a (3D) camera).

6. Conclusion

Numerous relationships between feeding patterns and growing-finishing pig welfare were identified. Reduced welfare states are mostly associated with deviations from basal feeding patterns. Physiological welfare problems strongly affect feed intake, and different types of physiological problems may induce varying deviations in the underlying feeding behaviours. Behavioural welfare problems are mostly reflected by changes in the underlying feeding behaviours, while feed intake remains relatively constant. This knowledge could be used to develop algorithms that can automatically relate pig feeding patterns to pig welfare, at the individual level. It appears promising to use several feeding behaviours simultaneously, using both group- and individual-level feeding patterns, at a short time scale (*i.e.* within a day). The outcomes of these algorithms could provide continuous rather than sporadic information on generic welfare, which could even be assessed and summarised retrospectively (*i.e.* after slaughter).

Nevertheless, it should be considered that a large variation in feeding behaviour is present between and potentially within pigs, and this variation should be well-understood before the variation that represents pig welfare can be interpreted. In addition, to get a good representation of pig welfare and to be able to distinguish between different causes of reduced welfare, more knowledge is required on the responses of the underlying feeding behaviours to different welfare problems, the effects of performing abnormal behaviours on feeding patterns and on how the affective aspect of welfare relates to pig feeding patterns.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.applanim.2021.105383.

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