

Understanding the feeding strategies of growing-finishing pigs: Exploring links with pig characteristics and behaviour

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ABSTRACT

A large variation in feeding patterns between pigs and over time hampers the use of data from electronic feeding stations in the continuous monitoring of growing-finishing pig welfare. Individual feeding strategies (i.e. differences between pigs that are consistent within a pig across time) likely explain part of this variation, both at the daily level - based on feeding components intake, frequency and rate - and at the diurnal level - based on feeding components circadian rhythms and night feeding. It is, however, not known exactly which feeding strategies pigs display, nor which types of pigs display which strategies. This study aimed 1) to test which (combinations of) feeding components contribute to independent feeding strategies; and 2) to see whether pigs with different feeding strategies also differ in other physical and behavioural characteristics. To identify feeding strategies, we calculated the intra-class correlation coefficient (ICC) for each day-level feeding component, which reflects the proportion of variation explained by an individual pig effect (n=98 pigs). Subsequently, high ICC day-level components were correlated to diurnal-level components known to contain feeding strategies, to assess possible overlap. Pigs with different strategies were then characterised based on physical (n=52) and behavioural (home pen and play tests, n=22–27) variables at different ages, using (generalised) linear mixed models. Four dimensions of individual feeding strategies emerged: nibbling/meal eating, fast/slow eating, day/day-night eating and consistent/inconsistent eating from day to day, sustaining after correction for pig sex or body weight. All dimensions except day/day-night eating partially overlapped at the beginning of the growing-finishing phase, but became more distinct over time. Pigs with different feeding strategies also differed in their general activity, diurnal activity and possibly dominance rank. Feeding strategies did not relate to behaviours possibly indicative of more positive or negative emotional states of pigs. Our results demonstrate that pigs showed individual differences in their feeding behaviour that are consistent across time, along continua in four distinct dimensions. These differences went beyond differences in body weight and sex, and were related to other behavioural characteristics of pigs. The presence of feeding strategies suggests that the use of pig feeding behaviour data should be corrected for individual differences between pigs.

1. Introduction

The feeding patterns of growing-finishing pigs (hereafter simply 'pigs') can be expressed using multiple components, including feed intake, feeding duration, feeding frequency, feeding rate, meal intake, meal duration and meal interval, aggregated at the daily level (i.e. per 24 h) (Maselyne et al., 2015; Nielsen, 1999). For most components, pigs change their feeding patterns when facing welfare issues. For example,

intake and duration reduce during infections (Helm et al., 2018b, 2018a; Schweer et al., 2016) and frequency is lower in pigs with osteochondrosis compared to healthy pigs (Munsterhjelm et al., 2017). Therefore, feeding patterns could constitute promising indicators of pig welfare (Bus et al., 2021). This is especially relevant when feeding patterns are monitored continuously with sensors, using computer vision, RFID antennas or electronic feeding stations (EFSs). Nevertheless, the development of algorithms that translate feeding data into welfare-relevant

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information is hampered by the large reported variation in feeding patterns between pigs and within pigs across time (Bus et al., 2021). Part of this variation is due to individual differences between pigs (Boumans et al., 2018a, 2018b), suggesting pigs apply feeding strategies. In this paper, feeding strategies are conceptualised as (combinations of) feeding components for which pigs differ from each other but are relatively consistent across time.

The most well-reported putative feeding strategies describe individual differences at the daily level. These feeding strategies did not identify clusters of pigs but rather placed pigs across two distinct continua, meaning that pigs gradually differed from each other between two extremes. One continuum ranged from so-called ‘meal eaters’ to ‘nibblers’, i.e. from pigs that eat large, infrequent meals to pigs that eat small, frequent meals, and the other from ‘fast eaters’ to ‘slow eaters’, i.e. pigs with respectively high and low feeding rates (Fernández et al., 2011; Garrido-Izard et al., 2020; Labroue et al., 1997, 1994). These strategies were largely identified using correlations between different components of feeding patterns, and it is hence not known whether pigs are consistent in a strategy over time. At the diurnal level, reflecting within-day feeding behaviour, we previously demonstrated pigs apply two types of feeding strategies (Bus et al., 2023a). First, pigs differed in the proportion of intake obtained at night, ranging from day eaters to day-night eaters, with ‘day’ and ‘night’ as consecutive hours of high and low feeder occupation. Second, pigs differed in how consistently they timed their feeding from day to day, ranging from consistent to inconsistent eaters. This suggests that pigs show consistent feeding strategies across the growing-finishing phase, however, this has not been confirmed for the proposed day-level strategies (i.e. nibbling/meal eating and fast/slow eating) nor for other day-level components (e.g.

duration, meal duration, meal interval). In addition, it is currently unclear whether these day- or diurnal-level feeding strategies overlap, as nibblers could for example be the same pigs as day eaters, and which types of pigs display which strategies.

A route to better understanding the differences in feeding strategies between pigs is by comparing these pigs along other characteristics, such as physical and behavioural characteristics. Some characteristics have already been compared to components of feeding patterns, indicating that day-level feeding components differ between pigs of different sexes (Fàbrega et al., 2010; Schmidt et al., 2011), body weights (Georgsson and Svendsen, 2002), and social ranks (Hoy et al., 2012; Leiber-Schotte, 2009), although the direction of the effect may depend on environmental characteristics of the pen and feeder (Gonyou and Lou, 2000; Morrow and Walker, 1994). Pigs could additionally be compared across behavioural characteristics, such as activity, exploration, play, tail postures/movements or social interactions, as well as using diurnal-level in addition to day-level feeding strategies. This could provide further insight into how pigs with different feeding strategies differ from each other, and could additionally be relevant from a welfare perspective as several behavioural characteristics have been associated with more positive or negative emotions.

The overarching aim of this study was to expand our understanding of the individual feeding strategies of growing-finishing pigs, with two sub-aims: 1) to understand which feeding components contribute to independent feeding strategies, and 2) to see whether pigs with different feeding strategies also differ in other physical and behavioural characteristics. An independent feeding strategy, here, is conceptualised as a (combination of) feeding component(s) for which pigs consistently behave differently from each other, and that does not overlap with other

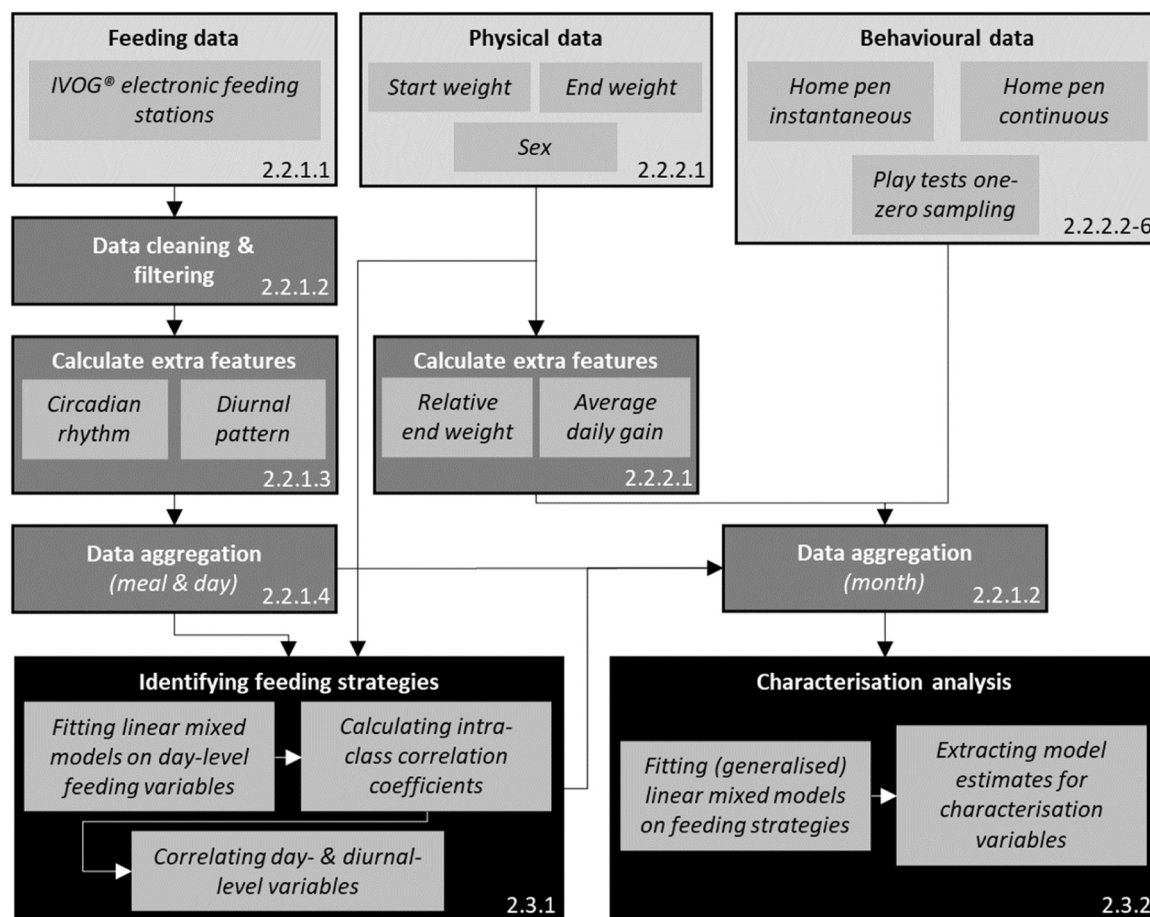


Fig. 1. Flow chart describing the process from data collection (light grey boxes) to data analysis (black boxes), specifying the steps of data processing (dark grey boxes) and the links between the different steps. Each step also specifies the section number in which more information can be found.

feeding strategies. This study is of an explorative nature, and aimed to obtain knowledge in a practical context that could reveal interesting pathways for further fundamental study.

2. Methods

An overview of the process of data collection, processing and analysis can be found in Fig. 1. In short, we used electronic feeding stations to collect data on the feeding behaviour of individual, but group-housed, pigs. These data were cleaned and aggregated to the daily level (i.e. per 24 h), and extra features were calculated at the diurnal level using hourly-aggregated data. An overview of all day- and diurnal-level feeding components along with their definitions is presented in Table 1. For the day-level feeding components, it was tested whether these components contribute to feeding strategies using the intra-class correlation coefficient (ICC). The ICC was calculated both before and after correction for body weight and sex, which are likely explanatory factors for individual feeding strategies. Subsequently, possible overlap between the day-level and diurnal-level components that were identified to contain individual consistency (for diurnal, this was done in previous research (Bus et al., 2023a)) was investigated using correlations. Based on these ICCs and correlation coefficients, components were selected and feeding strategies were identified, and strategy-relevant components were further compared against a range of physical and behavioural characterisation data using (generalised) linear mixed models, at the monthly level. The monthly level was chosen to obtain results in an interpretable format while still capturing possible age effects.

2.1. Animals and housing

This observational study was performed on commercially-reared growing-finishing pigs, complying with relevant EU and German guidelines and regulations. As no invasive or harmful procedures were

Table 1

Units and definitions of all day-level and diurnal-level feeding components included in this paper. Day-level components were calculated directly from the feeding station data by summing or averaging meal-level measurements. Diurnal-level components were calculated using hourly-level sums of visit intakes which were processed using either generalised additive models (GAMs), to quantify diurnal variation, or using wavelet analyses, to detect circadian rhythms.

Feeding component	Unit	Definition
Day-level feeding components		
Intake	kg	Total daily feed intake; the sum of the feed intakes of each meal.
Duration	s	Total daily feeding duration; the sum of the feeding durations of each meal.
Frequency		The number of nutritive meals on this day.
Rate	g/s	The speed with which a pig ate its nutritive meals; intake divided by duration.
Meal intake	kg	The average of the feed intakes of each meal.
Meal duration	s	The average of the durations of each meal.
Meal interval	s	The average of the intervals between each meal and the next.
Diurnal-level feeding components		
Proportion of intake obtained at night		From the GAM predictions, the intake obtained between 21:00–04:59 h divided by the intake obtained during the full 24 h.
Highest probability to eat		From the GAM predictions, the proportion of days within the self-defined period on which the pig ate during a certain hour, for the hour on which the pig most frequently ate (i.e. the largest proportion of days).
Number of days with a circadian rhythm		From the wavelet analysis, the number of days within the self-defined period on which behavioural repetition at 23.5–24.5 h was detected.

applied, ethical approval for animal experimentation was not required according to Dutch (Article 1 Wet op de Dierproeven, 2021, <https://wetten.overheid.nl/BWBR0003081/2021-07-01>) and German (Article 7 Tierschutzgesetz, 2022, <https://www.gesetze-im-internet.de/tierschg/BJNR012770972.html>) legislation.

We studied one round of tail-docked growing-finishing pigs (Piétrain x (Landrace x Large White), n=110), reared between December 2020 and March 2021 at a Topigs Norsvin (pig breeding company, the Netherlands) growing-finishing farm in Germany. Pigs were observed from arrival at the farm until the day of transport to be slaughtered, with the first batch of heaviest pigs slaughtered after 83d (eight days after final weighing of all pigs at 107 ± 8.7 kg (mean \pm standard error)). Pigs were housed in single-sex pens (n=11 pigs/pen) across five rooms, with one pen with barrows and one pen with gilts in each room. Each pen was equipped with an IVOG[®] EFS (Hokofarm group, the Netherlands), from which pigs could obtain pelleted feed *ad libitum* (until d33, Select Delta 2: 16.2% crude protein (CP) and 13.2 MJ/kg metabolisable energy (ME); between d33–64, Select Delta 4: 15.3% CP and 13.1 MJ/kg ME; post d64, Select Delta 5: 13.8% crude protein and 13.0 MJ/kg ME (feed was mixed for 2–3d upon every switch); all produced by Royal Agrifirm Group, the Netherlands). Additionally, each pen was equipped with two drinking nipples providing *ad libitum* access to water, fully slatted floors, and a combination of a hanging wooden block, chains with plastic rings and hanging ropes intended as enrichment (enrichment differed between pens and across time). Temperature gradually reduced from approximately 25°C to 22°C across the growing-finishing phase, with a diurnal variation of 1–2°C and largest difference between rooms of approximately 2°C. Artificial lighting was not provided, except during human presence in the room. Instead, windows provided natural lighting with the approximate number of daylight hours increasing from 8 to 12.5 h across the growing-finishing phase. All management procedures were determined and performed by Topigs Norsvin employees, whose animal caretaker checked on the pigs twice daily. Three pigs had to be moved to a sickbay before reaching slaughter weight due to health issues (after d10, d49 and d75, the latter two from the same pen), and were hence removed from the study before completion. No pigs received medical treatment before being moved to the sickbay.

2.2. Data collection and processing

All data processing and analyses were performed in R, version 4.2.3 (R Core Team, 2023). Figures were created using the *ggplot2* package (Wickham, 2016) and tables using the *flextable* package (Gohel and Skintzos, 2023).

2.2.1. Feeding data

2.2.1.1. Feeding data collection. Feeding data of each pig throughout the growing-finishing phase were collected using IVOG[®] EFSs. These EFSs are single-space feeders without protective crates for the feeding pig. A small fence prevents pigs from entering the EFS simultaneously and a metal bar on the floor prevents pigs from lying down in the EFS. Each EFS contains an RFID antenna and a load cell to identify the feeding pig and to measure the quantity of feed consumed. When a pig entered the feeder, its electronic ear tag was detected by the RFID antenna and its unique transponder number was registered. Simultaneously, the time stamp of entrance and, as feed is always present in the trough, the weight of the feed in the trough were recorded. Trough weight and the time stamp were recorded again when the pig exited the feeder, and from this the intake (difference in trough weight between feeder entrance and exit, in kg) and the duration (difference between entrance and exit time stamps, in s) were extracted. The feeding trough was filled automatically from a reservoir on top whenever the trough weight went below a fixed threshold, and if a pig began feeding during a filling its intake was corrected for the filling. From the visit intake and duration,

we could calculate the rate (intake/duration * 1000, g/s) and the interval to the previous feeder visit (s). This provided a dataset consisting of 219,521 visits for 110 pigs.

2.2.1.2. Feeding data cleaning. As EFSs are known to sometimes make incorrect registrations, a cleaning algorithm was developed to remove putatively incorrect visit registrations from the feeding data. This process removed visits based on missing RFID numbers, extreme values for intake, duration and rate, impossible weight differences of the feed in the trough between successive visits, and overlapping time stamps. Thresholds for extreme values were obtained from literature (based on those of Casey et al. 2005 and Eissen et al. 1998) and checked against visualisations of our data, and if no literature was available thresholds were determined directly from our visualisations. If only the data from the load cell appeared compromised, intake and rate were removed but duration and visit interval were retained. If more than 15% of a pig's feeder visits on a certain day were fully or partially removed, all visits from that pig day were removed to avoid deviating data after aggregation to larger timeframes (e.g. hourly or daily data). The algorithm steps and number of visits removed at each step are described in detail in Sections 1 and 2 of the Supplementary Methods of Bus et al. (2023a). Its application led to the removal of 7.27% of all visits (of which 5.48% fully removed, and 1.79% only intake and rate removed), leaving a total of 203,572 uncorrected visits.

To get as close as possible to 'basal' feeding data, we removed all visits on pig days (i.e. data of a specific pig on a specific day) that could be expected to be deviating from 'normal' behaviour. This mostly concerned days on which pigs were diseased, as identified using health observations performed by a single observer twice per week throughout the growing-finishing phase. The protocol for the health observations can be found in the DANS database (Bus et al., 2023c), although a previous version of the protocol was used in which lying bumps and conjunctivitis were not yet scored. Days surrounding pig-level health issues exceeding pre-set severity thresholds (see Supplementary Methods of Bus et al. 2023a) were removed from the feeding data from 3d before to 3d after observation, leading to a total of 916 pig days removed (12.5% of the total pig days available), mostly due to ear damage (439d), tail damage (278d), flank damage (150d) and lameness (127d). Additionally, data from one pen were fully removed due to an ear-biting outbreak shortly after arrival followed by a tail-biting outbreak until slaughter (757 pig days). Finally, 326 pig days were removed because they occurred before the first health observations were performed, and 539 pig days because they occurred after the date on which the heaviest pigs were transported to be slaughtered, as the remaining pigs were likely impacted by social disturbance of the removal of pen mates. The process is described in detail in the Supplementary Methods of Bus et al. (2023a). The final dataset consisted of 6348 complete days (68% of available pig days) on 98 pigs from 9 pens, with a median of 65 days per pig (range 16–79d).

2.2.1.3. Obtaining diurnal features. The cleaned visit data can be aggregated directly to obtain daily features (described later in Section 2.2.1.4), but in addition to the daily features we wanted to obtain features describing the diurnal feeding strategies of pigs. Therefore, before aggregation we used the hourly intake (kg, sum of all visit intakes in an hour) to calculate components that reflected the diurnal pattern of feeding activity and the day-to-day consistency in this diurnal pattern. These components were chosen based on our previous work (Bus et al., 2023a), in which we demonstrated that pigs displayed consistent variation (i.e. feeding strategies) in the proportion of intake obtained at night, the number of days with a circadian rhythm in feeding behaviour and the highest probability to eat - a measure of how consistently a pig eats at a certain time of day. Details on the calculation of these components are presented in Bus et al. (2023a), and a short overview is provided here.

The strength of pigs' circadian rhythms in feeding was detected using wavelet analysis, which is capable of detecting repetitions in a time series at a range of different periodicity - our interest was at a periodicity of 24 h, i.e. circadian. Wavelet analysis was applied on the hourly intake data of each pig separately. Hourly intake data were first de-trended by fitting a local regression model (*loess* function of the *stats* package (R Core Team, 2023)) with a span of 0.75, from which the residuals of the fit were extracted for use in further analysis. Subsequently, the data were corrected for amplitude changes by extracting the difference between the highest and lowest hourly intake for every 7d and dividing each data point within the 7d window by this difference, and missing data were replaced by zero values. Wavelet analysis was performed with the R package *WaveletComp* (Roesch and Schmidbauer, 2018), using a Morlet base wavelet and a continuous wavelet transform. For each moment in the time series, we obtained the power of the repetition at a range of periodicities, representing the strength of the repetition, and significance of the power was estimated using a comparison between the power on the hourly intake data and a thousand simulations of white noise. From this, the median of the P-values on the 24 time points (hourly intake) of the day between frequencies 23.5–24.5 h was taken, and a day was noted as showing a circadian rhythm if this median P-value was smaller than 0.05.

Generalised additive models (GAMs, R package *gamlss* (Rigby and Stasinopoulos, 2005)) were used to model the diurnal patterns of each pig separately, which provided us with a continuous quantification of the diurnal pattern from which the proportion of intake obtained at night and the highest probability to eat could be extracted. The GAM modelled the overall trend in intake across the growing-finishing phase (i.e. the increase in intake with age, modelled with a spline with four knots) and added diurnal patterns, split into pre-set periods, as hourly variation surrounding this trend (modelled as a cyclical spline with eight knots). The pre-set periods differed between the research questions, as described in Section 2.3. Zero- and non-zero data were modelled separately, using a hurdle model that fitted both the probability of a pig eating (logistic regression with a logit link) and subsequently intake as a continuous response weighted for the probability of eating (zero-adjusted gamma (ZAGA) with a log link). Model fit was checked by plotting model predictions on top of the raw data. From the results of the GAM model, the proportion of intake obtained at night was calculated as the predicted intake obtained between 21:00–04:59 h divided by the total predicted intake, and the highest probability to eat as the maximum of the probability fit of the hurdle model. The highest probability to eat thus reflected the proportion of days within the period that a pig was eating at a certain time within the period, with a high proportion meaning that a pig consistently ate at that time.

2.2.1.4. Feeding data aggregation. After cleaning and calculation of diurnal features, the feeding visit data were aggregated to the meal level using a meal criterion of 43 s, meaning that all visits separated by intervals shorter than 43 s and during which no pen mate had entered the feeder were summed into a single meal (Bus et al., 2023b). This meal criterion was calculated as the intersection of the first two curves (Bus et al., 2023b) of a three-part (two Gaussians and one Weibull) probability density function fitted to the log-transformed visit intervals, as described in detail in Tolkamp et al. (2000), (1998) and Yeates et al. (2001). During the aggregation, meal intake (kg) was calculated as the sum of the visit intakes (if intake was missing for one of these visits, the missing intake was regarded as 0 kg), meal duration (s) as the difference between start time of the first visit and the end time of the last visit, meal interval (s) as the difference between the start of the current meal and the end of the previous meal, and rate (g/s) as the newly calculated meal intake divided by the meal duration, multiplied by one thousand (if either intake or duration was missing or zero, no rate was calculated). After aggregation to the meal level, the data were further aggregated to the daily level, giving daily intake (kg) and daily duration (s) as the sum

of meal intake and meal duration, respectively, the meal frequency as the number of meals in that day, and the average meal intake (kg), meal duration (s), meal interval (s) and rate (g/s) as the means of the corresponding components.

2.2.2. Characterisation data

The characterisation data, against which the feeding data were compared, consisted of physical and behavioural data.

2.2.2.1. Physical. Physical data concerned pig body weight, which was measured for each individual pig using a weighing scale (Welvaarts Weegsystemen W-2000, The Netherlands, accuracy ± 0.5 kg) upon arrival at the farm (d1) and 8d before the first pigs were slaughtered (d75). From this, for each pig we calculated the average daily gain (ADG) as the difference between end and start weight divided by the number of days between the weighing moments. We also calculated for each pig the body weight relative to its pen mates by dividing the end weight by the average end weight of all pigs in the pen. This allowed us to distinguish between direct effects of body weight and effects related to social dynamics, where the relevance of a pig's body weight depends on the weight of its pen mates.

2.2.2.2. Behavioural - in general. Behavioural data were scored manually from videos obtained using Lorex 4 K Ultra HD Smart Deterrence (8MP) cameras (Lorex Corporation, Canada) installed on the wall of the pen (1 or 2 cameras per pen) at a height of approximately 2 m. Pigs were marked individually during the health observations, using coloured sprays on their backs, to enable individual identification from video. Behavioural observations were performed in each month, to be able to account for age effects, with two days scored per month. These days were always either on the day of the health observations (behavioural observations related to the play tests) or the day after (behavioural observations in undisturbed situations in the home pen), as the spray marks were then sufficiently recognisable from video.

All behavioural observations were performed on thirty focal pigs from six pens (five pigs/pen), which were selected based on diversity in their feeding patterns and data availability in the middle of the growing-finishing phase (i.e. month 2). Based on feeding data from month 2, sequentially, the most extreme pig within each pen was selected for 1) nibbling (highest value for frequency/meal intake), 2) meal eating (lowest value for frequency/meal intake), 3) eating at night (highest proportion of intake between 20:00–07:59 h), 4) eating in the morning peak (highest proportion of intake between 08:00–12:59 h), and 5) eating in the afternoon peak (highest proportion of intake between 13:00–19:59 h). If a pig appeared to have missing feeding data in the period of the behavioural observations (in month 2) or if the pig had already been selected for a strategy earlier in the process, the next most extreme pig was chosen until 30 pigs with complete data in month 2 were obtained. Some selected pigs had missing data in months 1 and 3 as too much feeding data was missing or the pig had been removed from the experiment early, therefore eventually in month 1 27 and in month 3 22 pigs were included in the analysis. On the selected pigs, three types of observations were performed: instantaneous observations, continuous observations, and one-zero sampling during play tests.

2.2.2.3. Behavioural - Instantaneous observations during 24 h. Instantaneous observations were performed on days 24 & 27 (month 1), 51 & 58 (month 2) and 79 & 80 (month 3). Behaviour was scored for each focal pig during 24 h of the day, using 10-min instantaneous scan sampling, in Microsoft Excel. Scored behaviours concerned general activity (i.e. locomotion, standing, sitting, kneeling and lying - all split as either active or inactive), behaviour at the feeding station (i.e. queuing), tail postures (i.e. erect, horizontal, active hanging or tucked), and tail movements (i.e. loosely wagging, intense wagging, jamming and no movement). For more details on their definitions, we refer to the full

ethogram in [Supplementary Table S1](#). Tail postures and movements were only recorded when a pig was standing or in locomotion, as during sitting, kneeling or lying down the observations of tail postures and movements are deemed unreliable (Camerlink and Ursinus, 2020). To score tail motions, the video was played at each scan for a few seconds. When a pig was out of view this was scored as such. Observations were performed by three trained observers with an inter-observer reliability (Cohen's kappa) of 0.72 (calculated as the average per category of mutually-exclusive behaviours and observer pair, based on in total 8 h of video of four different pens (five pigs/pen) selected for high occurrence of active and low-occurring behaviours), after removal of queuing, which was deemed unreliable between observers and hence not further analysed.

2.2.2.4. Behavioural - Continuous observations during the most active hours. Continuous observations were performed on the same days as the instantaneous observations (d24, d27 (month 1), d51, d58 (month 2), d79 & d80 (month 3)), during the three most active hours (i.e. two times 3 h per month). The most active hours were selected using the instantaneous observations, by identifying the three hours with the highest average occurrence of 'upright active'. The selected most active hours were: 10:00–10:59 h, 14:00–14:59 h and 16:00–16:59 h in month 1; 10:00–10:59 h, 15:00–15:59 h and 17:00–17:59 h in month 2, and 15:00–17:59 h in month 3. Within these hours, behaviours of each focal pig were scored continuously using BORIS (Friard and Gamba, 2016) by three trained observers with an inter-observer reliability (Cohen's kappa) of 0.69 (calculated using the built-in function of BORIS with 1 s intervals, based on in total 6 h of video of three different pens (five pigs/pen) selected for high occurrence of active and low-occurring behaviours). Scored behaviours concerned general activity (i.e. lying inactive and exploring pen), behaviour at the feeding station (i.e. displacing either with or without aggression), social interactions (i.e. nose-nose contact, nose-body contact, aggressive acts, fighting, displacing either with or without aggression, tail manipulation, ear manipulation, belly nosing and mounting), and play (i.e. locomotor, social and object play). For the complete ethogram we refer to [Supplementary Table S2](#). For antagonistic social interactions, displacements and damaging behaviour, both the performing and the receiving pig were recorded. If a pig was not well visible for either receiving or performing, this was scored as being out of view for receiving or performing, respectively.

2.2.2.5. Behavioural - One-zero sampling during play tests. Play occurs little in growing-finishing pigs in their home pens, but is thought to be a promising indicator of positive emotion (Ahloy-Dallaire et al., 2018). Therefore, we applied play tests to elicit play behaviour. From d43 onwards, play tests were performed twice a week immediately following the health observations. The order in which rooms were tested was randomised before the first play test and this order was maintained until the end of the experiment. Once the health observations in a room were completed, toys were placed in the home pens in a standardised manner and were left for 45–60 min for the pigs to interact with, after which they were removed again. The toys consisted of 1) a spike ball (green, 9 cm diameter with 12 spikes of 15.5 cm each, 2.3 kg), 2) a ball (yellow, 25 cm diameter, filled with sand up to 2.2 kg of total weight), 3) a short (1 m) and 4) a long (1.5 m) hose pipe (yellow, 4.5 mm diameter), and a tightener attached diagonally across the pen at 110 cm height from which hung 5) a dog chewing rope (black, grey & white, 66 cm long, 7 cm thick, with four knots) and 6) a chain with a horizontal stick (blue, 2.5 cm long, 3.3 cm thick, chain length adapted to have the stick hanging at pig head height). Photographs of the play test and the toys are provided in [Supplementary Figure S1](#). Behavioural observations were performed on days 51 and 58 (month 2) and 78 and 82 (month 3) using BORIS (Friard and Gamba, 2016). A single observer recorded general activity (i.e. object interaction), tail postures (i.e. erect,

horizontal, active hanging or tucked) and movements (i.e. loosely wagging, intense wagging, jamming and no movement) and markers of object (i.e. holding, shaking, carrying or throwing a toy), locomotor (i.e. scampering, pivoting, turning, hopping, flopping and head tossing) and social play (i.e. chasing, pushing, nudging, self-handicapping). The full ethogram is presented in [Supplementary Table S3](#). Behaviours were scored during the 10 min immediately following the exit of the experimenter who placed the toys in the pen, using one-zero sampling with 5 s intervals (i.e. each behaviour that occurred at some point within these 5 s was scored as 'yes'). Like before, tail postures and movements were only scored if a pig was standing or in locomotion, and if a pig or its interaction with the toy was not well visible this was scored as out of view.

2.2.2.6. Behavioural - Data processing. All scored behaviours were aggregated to monthly levels and expressed as proportion of observed scans, time or periods, corrected for the time spent out of view or, for tail postures and movements, not applicable. To reflect diurnal activity, additional variables were created based on the general activity scores of the instantaneous sampling. These were called day active and night active, and were calculated as the sum of all active (i.e. standing, sitting, kneeling and lying active plus locomotion) behaviours during the day (05:00 h–20:59 h) or night (21:00–04:59 h). Due to low occurrence (or high occurrence, in case of erect tails), several behaviours had to be merged or could not be analysed. All active postures (instantaneous observations) except lying were merged into 'upright active' (locomotion and standing, sitting, and kneeling active); inactive postures (instantaneous observations) except lying were merged into 'upright inactive'; aggressive and non-aggressive displacements (continuous observations) were merged; all types of play (both continuous observations and play tests) were merged; ear and tail manipulation (continuous observations) were merged; and low tail postures (active hanging and tucked in play tests) were merged into 'low tail', to which jamming was added as well due to difficulty in distinguishing jamming from tucked tails. Behaviours that could not be analysed at all due to low occurrence included all tail postures and movements in the instantaneous observations except loosely wagging, and belly nosing and mounting from the continuous observations.

2.3. Data analysis

2.3.1. Identifying feeding strategies

The strength and independence of feeding strategies was studied using two methods: 1) calculating the intra-class correlation coefficient (ICC) for day-level feeding components, and 2) correlating day- and diurnal-level components with high ICCs against each other to see whether they overlap and should be considered a single strategy.

2.3.1.1. Intra-class correlation coefficients for day-level feeding components. The ICC is calculated using linear mixed models and is also referred to in literature as the behavioural repeatability (Bell et al., 2009). In this set-up, it reflects the proportion of variation in the data explained by the random effect of pig, corrected for other fixed factors included in the model. If the ICC is high, pigs differ from each other in a consistent way, while if the ICC is low pigs are either similar to each other or are inconsistent in how they behave over time. High ICC values, hence, support the existence of feeding strategies. We fitted three linear mixed models (function *lmer()* from the *lme4* package (Bates et al., 2015)) for each day-level feeding component: intake (kg), duration (s), frequency, rate (g/s), average meal intake (kg), average meal duration (s) and average meal interval (s). For all models, the response variable was the feeding component explained by a fixed effect of the number of days in the barn (i.e. to correct for age) and random effects of pig and pen. The first model contained no additional variables, the second model had an additional fixed effect of sex and the third had an additional fixed

effect of body weight at the final weighing (i.e. d75, 8d before transport to be slaughtered), to explore which part of the individual variation could be explained by the pig's sex or body weight and whether feeding strategies could still be identified independent of the pig's sex or body weight. All components except intake were log-transformed to meet normality assumptions, checked using a histogram, qq-plot and Shapiro-Wilk test ($W > 0.9$) on the raw data and model residuals. The ICC was calculated for each combination of fixed factors and feeding components by dividing the proportion of variation explained by the pig effect by the total variation, which was the sum of the pig, pen and residual variation. Subsequently, a 95%-confidence interval around the ICC estimate was approximated using posterior simulations of the model (1000 repetitions, function *sim()* from the *arm* package (Gelman and Su, 2022)). ICCs were compared numerically and were interpreted as weak (> -0.4 and < 0.4), moderate (≤ -0.4 and > -0.6 , or ≥ 0.4 and < 0.6) or strong (≥ 0.6 or ≤ -0.6).

2.3.1.2. Correlating day- and diurnal-level feeding strategies. To check for possible overlap between day- and diurnal-level components with moderate to strong individual consistency, spearman correlation coefficients were calculated for five 2w-periods between all day-level and diurnal-level feeding components that had an ICC higher than 0.4, using the *rcorr()* function of the *Hmisc* package (Harrell Jr., 2023). Periods of 2w (14d, minimum of 7d of data available for a pig period to be included) were used because diurnal-level components (i.e. proportion of intake obtained at night, number of days with a circadian rhythm and the highest probability to eat) could not be calculated for each day. For day-level feeding components (i.e. intake, duration, frequency, rate, meal intake, meal duration and meal interval), aggregation to periods of 14d was achieved by taking the median of the day-level equivalent. For diurnal-level feeding components, aggregation was done by calculating the proportion of days with a circadian rhythm (as described previously, 'wavelet analysis'), and fitting the GAMs using periods of 14d. Correlation coefficients were for each period interpreted as weak (> -0.4 and < 0.4), moderate (≤ -0.4 and > -0.6 , or ≥ 0.4 and < 0.6) or strong (≥ 0.6 or ≤ -0.6).

2.3.2. Links with characterisation parameters

Associations between feeding strategies (i.e. feeding components with at least a moderate ICC and at most a strong correlation with another component that was not part of the same strategy) and characterisation variables (i.e. physical and behavioural variables) were tested with (generalised) linear mixed models, fitted with the *glmmTMB* package (Brooks et al., 2017). Feeding data surrounding the periods in which characterisation data were obtained were selected, to narrow the feeding data to the same period as the physical and behavioural observations. We studied 5 periods of varying length (P1: d5–17, P2: d18–31, P3: d32–46, P4: d47–60, P5: d61–69, P6: d70–83), selecting the second, fourth and sixth period for analysis (i.e. months 1, 2 and 3, respectively). As before, aggregation was achieved using the median for day-level components, and for the diurnal-level components by calculating the number of days with a circadian rhythm within the period and by applying the stated periods into the GAM models. Subsequently, for each combination of a feeding component and a characterisation variable, a (generalised) linear mixed model was fitted with the feeding component as the outcome variable; month, the characterisation variable and the interaction between these two as fixed effects; and pig and pen as random effects (i.e. repeated measures). Normality assumptions were checked on the raw data and the model residuals, and model fits were checked by plotting the predicted against the raw data. If necessary, feeding components were log-transformed to meet normality assumptions (frequency, meal intake and rate). For the physical characterisation variables (ADG & relative body weight), data were only available in month 3, hence the random effect of pig, the fixed effect of month and the interaction effect were not included in the model, leaving only the

fixed effect of the characterisation variable and the random effect of pen. In addition, for relative body weight the random effect of pen was removed from the model. For the number of days with a circadian rhythm, normality assumptions could not be met. Therefore, this response was modelled as the proportion of days with a circadian rhythm (as a matrix with two columns: the number of days with and without a circadian rhythm) using a generalised linear mixed model with a betabinomial family distribution (logit link). In addition, for one model (feeding component: meal intake; characterisation variable: tail wagging in the play test) no convergence could be obtained with the standard setting, hence for this model a different optimisation algorithm (BFGS) was used which converged adequately.

For each model, a χ^2 -test was used to establish significance of the effects of the characterisation variable, period and their interaction on the feeding component (*Anova()* function from the *car* package (Fox and Weisberg, 2019)). The significance level was set at $P < 0.05$. If a significant interaction was observed, functions *test()* and *emtrends()* from the *emmeans* package (Lenth, 2022) were used to extract the model estimate of the characterisation variable for each month separately, testing significance with a t-test. If no significant interaction was observed, the interaction term was removed from the model and model estimates and errors of the estimates were extracted for the characterisation variable and period along with their significance as determined with the χ^2 -test. To allow for comparison of the model estimates between the different characterisation variables within a feeding component (note: not between feeding components), all characterisation variables were scaled by deducting the variable's mean from each observation and dividing it by the variable's standard deviation (*scale()* function (R Core Team, 2023)) before models were fitted. Because of the relatively large number of tests on the same data (9 feeding components and 30 characterisation variables gives $9 \times 30 = 270$ fitted models) and the associated enhanced chance of Type I errors, P-values were adjusted for each feeding component separately by listing all relevant characterisation-related P-values (one for models without interaction, 2–3 (one per period) for models with interaction) and applying False-Discovery-Rate correction (*p.adjust()* function from the *stats* package, method = "fdr" (R Core Team, 2023)).

3. Results

3.1. Identifying feeding strategies

All feeding components were associated with the number of days that pigs had been in the barn (all $P < 0.001$). Gilts had a lower intake ($\chi^2 =$

61.4, $P < 0.001$), duration ($\chi^2 = 14.2$, $P < 0.001$) and meal intake ($\chi^2 = 5.5$, $P = 0.019$) than barrows, but sex had no effect on meal duration ($\chi^2 = 2.8$, $P = 0.093$), rate ($\chi^2 = 0.3$, $P = 0.591$), frequency ($\chi^2 = 0.1$, $P = 0.697$) or meal interval ($\chi^2 = 0.0$, $P = 0.867$). Body weight was associated with all feeding components (all $P < 0.001$) except duration ($\chi^2 = 0.6$, $P = 0.457$), where heavier pigs had a lower frequency ($\chi^2 = 12.8$, $P < 0.001$) and a higher intake ($\chi^2 = 123.1$, $P < 0.001$), meal duration ($\chi^2 = 12.1$, $P < 0.001$), meal intake ($\chi^2 = 40.4$, $P < 0.001$), meal interval ($\chi^2 = 12.2$, $P < 0.001$) and rate ($\chi^2 = 30.2$, $P < 0.001$). The corresponding ICCs are shown in Fig. 2. When only day number was included as a fixed effect, ICC was weak for intake, moderate for duration, meal duration and meal interval, and strong for frequency, meal intake and especially rate. Correcting the ICCs for sex (i.e. if sex was added to the model as a fixed factor) had only marginal effects on the ICCs, giving a slight increase for duration, intake, meal duration and meal intake, but did not change their interpretations as weak, moderate or strong. In contrast, correcting the ICCs for body weight led to a noticeable reduction in the ICCs of rate and intake, although their classifications remained weak and strong respectively, and mildly reduced the ICCs for frequency and meal intake to moderate.

At least moderate ICCs were found for all day-level feeding components except daily intake, whether corrected for gender, body weight or neither (Fig. 2). Therefore, all feeding components except intake were included in further analysis. Correlations between day- and diurnal-level feeding components are shown in Fig. 3. There were strong correlations between the highest probability to eat - an indicator of day-to-day consistency in the timing of feeding - and frequency (positive), meal interval (negative), and meal intake (negative) in most periods, although the correlations became weaker with age. The highest probability to eat was also moderately negatively correlated with meal duration, and with rate in the first half of the growing-finishing phase. The proportion of days with a circadian rhythm showed similar correlations but weaker, giving moderate correlations with frequency (positive), meal interval (negative), meal intake (negative) and sometimes meal duration (negative), again becoming weaker with age. There were no correlations with the proportion of intake obtained at night, nor was duration correlated with any of the diurnal-level components.

3.2. Links with characterisation variables

Considering the similarity in the correlations between the day-level components frequency, meal interval, meal intake and meal duration and the diurnal-level components, it is likely that these four day-level components all reflect the same feeding strategy: nibbling versus meal

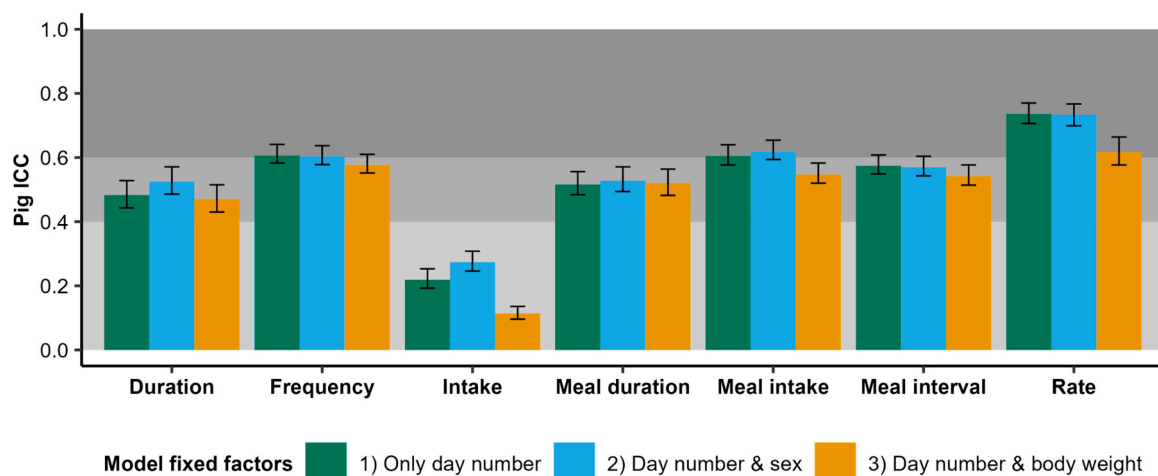


Fig. 2. Intra-class correlation coefficients (ICCs) of the effect of pig corrected for only the number of days in the barn (green), both the number of days and gender (blue) or both the number of days and body weight (yellow). ICCs with a shaded light grey background are interpreted as weak (ICC < 0.4), those with a shaded dark grey background as strong (ICC > 0.6) and those in between as moderate.

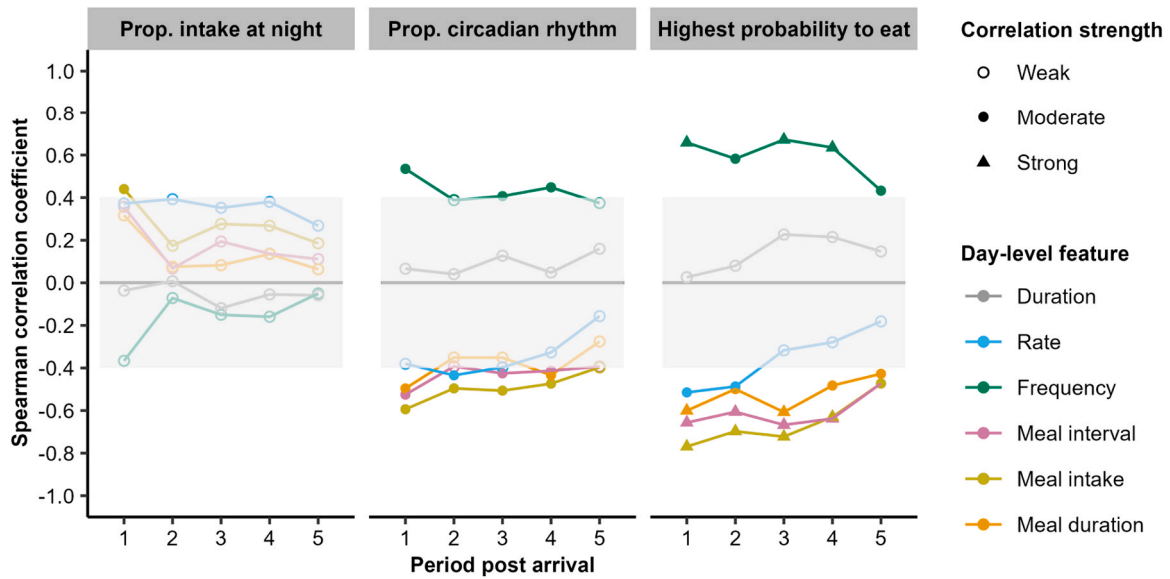


Fig. 3. Spearman correlation coefficients for each combination of diurnal-level (different facets, Prop: proportion) and day-level (different coloured lines) plots across the five 14d-periods of the growing-finishing phase. Correlation strength (weak: > -0.4 or < 0.4 ; strong: ≥ 0.6 or ≤ -0.6 ; moderate: in between) is shown with shapes and additionally weak correlations are greyed out. All correlations > 0.2 or < -0.2 were significantly different from zero ($P < 0.05$).

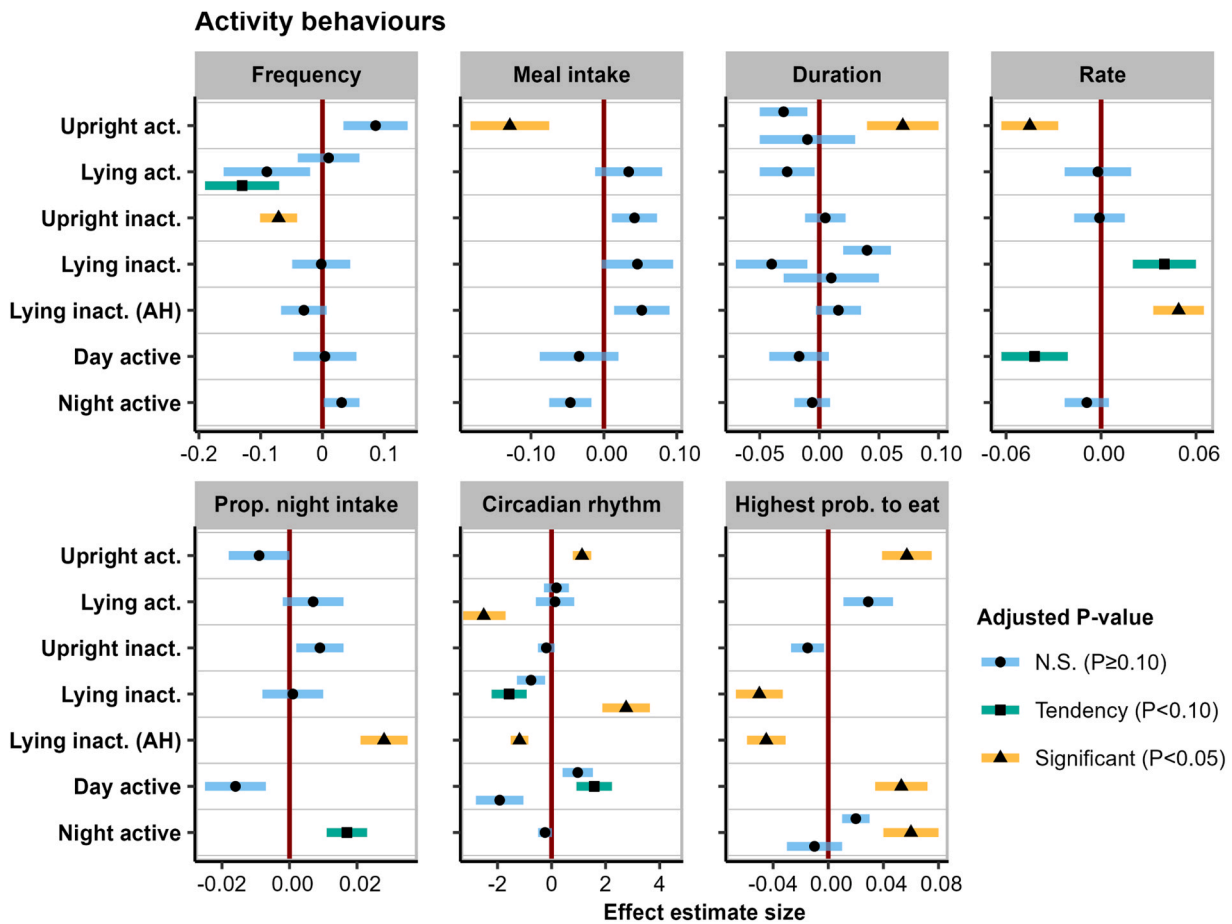


Fig. 4. Model estimates (dots) and error intervals (coloured bars) of the associations between feeding strategies and activity-related behaviours ($n=30$; act. = active, inact. = inactive) throughout the day and during the most active hours (AH). If there was an interaction between the behaviour and month ($P < 0.05$), model estimates are given for each month 1, 2 and 3 from top to bottom ($n=27$, $n=30$ and $n=22$, respectively). Model estimates significantly different from zero (red vertical line) after P-value adjustment are shown using shapes and colours.

eating. To reduce the number of tests applied, and hence reduce the chance of false positive results, we therefore selected only the two most commonly used to distinguish nibbling and meal feeding - frequency and meal intake - for comparison with physical and behavioural characteristics of pigs. Descriptive statistics (mean, standard error of the mean and range) for each feeding component and characterisation parameter are provided in [Supplementary Tables S4–6](#). Out of 210 performed tests (7 feeding components and 30 characterisation variables), after P-value adjustment there were 18 models with a significant association between the characterisation variable and the feeding component, and 20 effects of the interaction between the characterisation variable and month on the feeding component.

3.2.1. Physical

Both ADG and relative body weight were not associated with frequency, duration, proportion of intake obtained at night, number of days with a circadian rhythm or the highest probability to eat (in month 3, all adjusted P-values > 0.10, n=52). Both did, however, show a positive association with meal intake (ADG: $\chi^2 = 10.1$, P = 0.003; relative body weight: $\chi^2 = 5.7$, P = 0.032) and rate (ADG: $\chi^2 = 23.7$, P < 0.001; relative body weight: $\chi^2 = 7.8$, P = 0.011) - i.e. larger and faster-growing pigs consumed their feed faster and in larger meals.

3.2.2. Behavioural

The associations between the behavioural characterisation variables and the seven selected feeding components are shown in [Figs. 4–7](#). Feeding components most frequently associated with characterisation variables concerned the proportion of days with a circadian rhythm, the highest probability to eat, rate and duration, followed by frequency and meal intake, and only sporadically by the proportion of intake obtained at night. Associations between feeding components and characterisation variables were mainly seen for activity-, exploration- and socially-related variables, and only little for tail-related variables.

Concerning activity-related behaviours ([Fig. 4](#)), pigs with a higher frequency spent less time upright inactive ($\chi^2 = 5.7$, P = 0.036), those with a higher meal intake spent less time upright active ($\chi^2 = 5.7$, P =

0.032), and those with a higher duration spent more time upright active in month 2 (t = 2.37, P = 0.045). Pigs with a higher rate spent more time lying inactive during peak activity hour at all ages ($\chi^2 = 9.4$, P = 0.004), and less time upright active ($\chi^2 = 6.4$, P = 0.022). Diurnally, pigs with higher feed consumption at night spent more time lying inactively during the most active hours ($\chi^2 = 17.1$, P = 0.002). Regarding day-to-day consistency, pigs with a stronger circadian rhythm spent more time upright active ($\chi^2 = 10.8$, P = 0.022) and lying inactive in month 3 (t = 3.13, P = 0.025), and less time lying inactive during the most active hours ($\chi^2 = 13.2$, P = 0.019) or lying active in month 3 (t = -3.11, P = 0.025). Pigs with a larger highest probability to eat (i.e. more consistent in timing of feeding from day-to-day) spent more time upright active ($\chi^2 = 9.7$, P = 0.011), were more active during the day ($\chi^2 = 8.0$, P = 0.017) and in month 2 also during the night (t = 2.72, P = 0.024), and spent less time lying inactive in general ($\chi^2 = 8.6$, P = 0.016) and during the most active hours ($\chi^2 = 11.2$, P = 0.009).

Exploration- or play-related characterisation variables ([Fig. 5](#)) were not associated with frequency, meal intake, duration, rate, the proportion of intake obtained at night and the number of days with a circadian rhythm. Pigs with a higher highest probability to eat (i.e. more consistent in timing of feeding from day-to-day) spent more time exploring in month 3 (t = 2.43, P = 0.043).

Social behaviours were not associated with frequency, duration or proportion of intake obtained at night ([Fig. 6](#)). Pigs with a higher meal intake were less frequently displaced from the EFS ($\chi^2 = 8.1$, P = 0.009). Pigs with a higher rate spent less time in nose-body contact with other pigs ($\chi^2 = 5.2$, P = 0.040), and received fewer aggressive acts ($\chi^2 = 7.6$, P = 0.011) and displacements from the EFS ($\chi^2 = 6.0$, P = 0.026). Pigs with a stronger circadian rhythm spent less time in nose-nose contact in month 3 (t = -2.95, P = 0.035) and received fewer displacements in the pen in month 2 (t = 3.40, P = 0.022), while pigs with a larger highest probability to eat were less often displacing pen mates from the EFS in month 3 (t = -2.75, P = 0.024) and spent more time manipulating the tails and ears of pen mates ($\chi^2 = 7.3$, P = 0.024).

Tail postures and movements were not associated with frequency, meal intake, the proportion of intake obtained at night, the number of

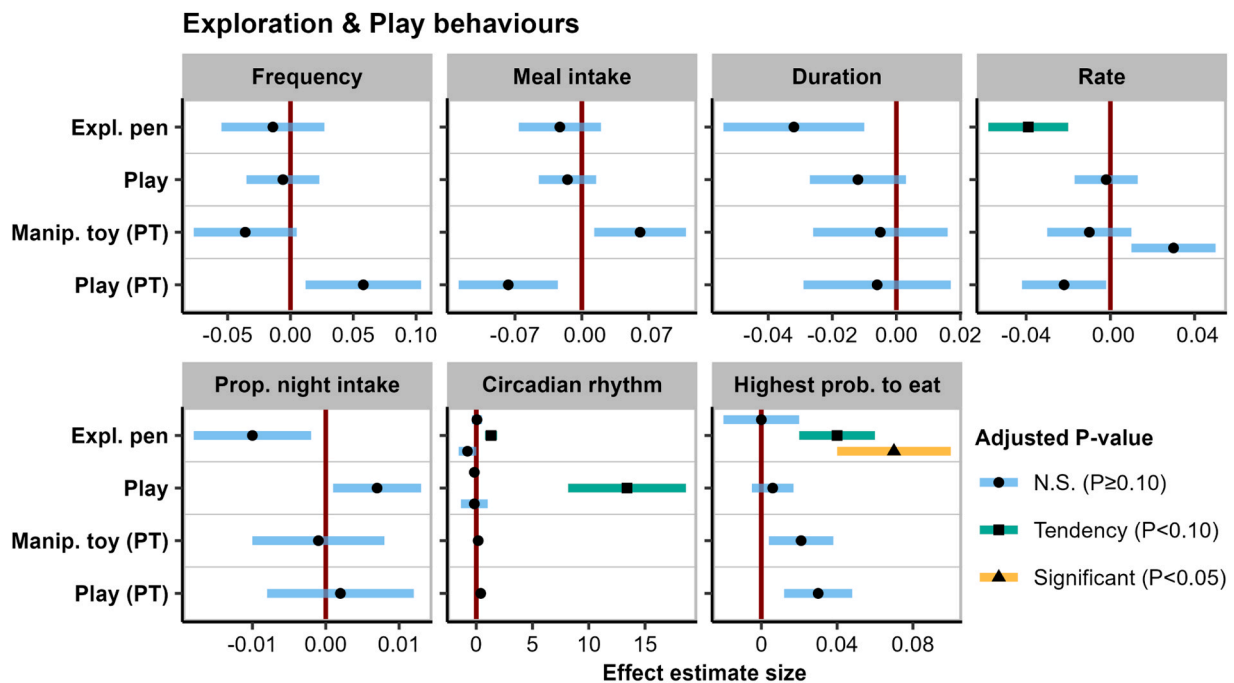


Fig. 5. Model estimates (dots) and error intervals (coloured bars) of the associations between feeding strategies and exploration- or play-related behaviours (n=30; expl. = exploring, manip. = manipulation) in the home pen and the play test (PT). If there was an interaction between the behaviour and month (P < 0.05), model estimates are given for each month 1, 2 and 3 from top to bottom (n=27, n=30 and n=22, respectively). For play test variables, only months 2 and 3 were included. Model estimates significantly different from zero (red vertical line) after P-value adjustment are shown using shapes and colours.

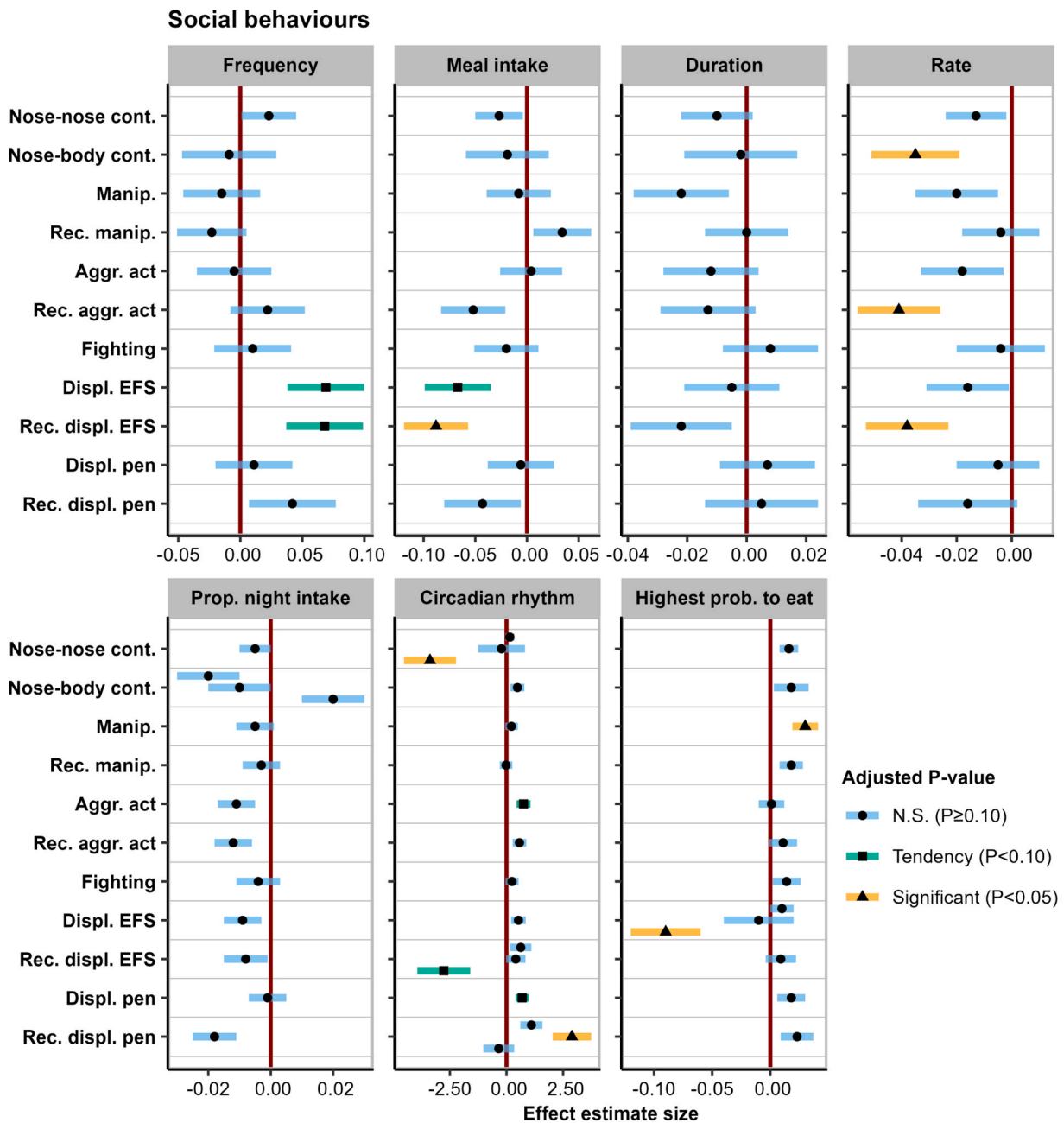


Fig. 6. Model estimates (dots) and error intervals (coloured bars) of the associations between feeding strategies and social behaviours (n=30; cont. = contact; manip. = manipulation; rec. = receiving, aggr = aggressive, displ. = displacement, EFS = Electronic Feeding Station). If there was an interaction between the behaviour and month ($P < 0.05$), model estimates are given for each month 1, 2 and 3 from top to bottom (n=27, n=30 and n=22, respectively). For play test variables, only months 2 and 3 were included. Model estimates significantly different from zero (red vertical line) after P-value adjustment are shown using shapes and colours.

days with a circadian rhythm or the highest probability to eat (Fig. 7). The only associations identified were that pigs with a lower duration ($t = -2.72, P = 0.021$) or rate ($t = -2.34, P = 0.041$) showed more frequent intense wagging in the play tests in month 3.

4. Discussion

This study applied an exploratory, two-step approach to expand our understanding of the individual feeding strategies of growing-finishing pigs. First, we tested which day-level components of feeding behaviour contribute to independent feeding strategies by calculating their intra-class correlation coefficients (ICCs) and comparing them to diurnal-level feeding components known to contribute to a feeding strategy. Second, we characterised pigs with diverse feeding strategies

along other physical and behavioural characteristics.

4.1. Identifying feeding strategies

Strong ICCs, indicating presence of individual feeding strategies, were found for frequency, meal intake and especially rate. These correspond to feeding strategies previously identified, related to meal eating/nibbling (i.e. frequency and meal intake) and fast/slow eating (i.e. rate) (Fernández et al., 2011; Garrido-Izard et al., 2020; Labroue et al., 1997, 1994). Additionally, duration had a moderate ICC, suggesting moderate consistency in how long individual pigs spend eating every day. For intake, no individual consistency could be identified, which suggests that either pigs are inconsistent in their intake across time – the most likely explanation based on visualisation of the ICC calculation

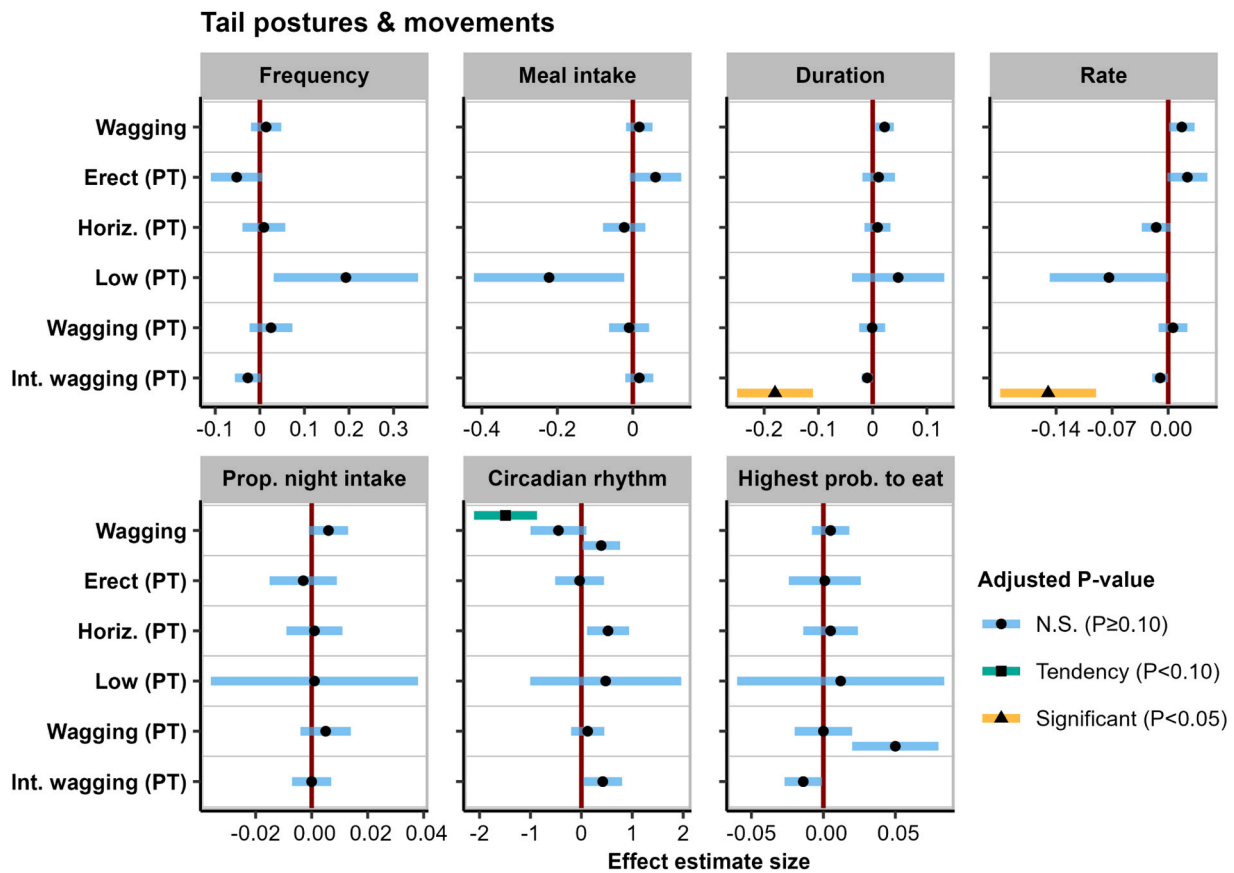


Fig. 7. Model estimates (dots) and error intervals (coloured bars) of the associations between feeding strategies and tail movements/postures ($n=30$; Horiz. = horizontal, Int. = Intense) in the home pen and the play test (PT). If there was an interaction between the behaviour and month ($P < 0.05$), model estimates are given for each month 1, 2 and 3 from top to bottom ($n=27$, $n=30$ and $n=22$, respectively). Model estimates significantly different from zero (red vertical line) after P-value adjustment are shown using shapes and colours.

(results not shown) – or there was little variation between pigs. The latter could be because pigs have been bred for optimal feed intake (Knap, 2009) and have hence become highly similar to each other, while the other feeding components have not undergone such rigorous genetic selection. As there was no individual consistency in intake, the moderate consistency in duration is likely part of the strategy of slow/fast eating, since rate is the reflection of intake and duration combined. Correcting for body weight reduced the ICCs of rate and meal intake, confirming that body weight influences strategies in these feeding components (Quiniou et al., 2000), but for other components and for pig sex, correction did not reduce the ICCs. These results suggest that pigs indeed show consistent individual differences in the day-level feeding components frequency, meal duration, meal intake, meal interval, duration and rate; either independent of body weight and sex or beyond what can be explained by body weight.

None of these six day-level feeding components were correlated with the diurnal-level component proportion of intake obtained at night, suggesting that they represented different dimensions of feeding strategies. The diurnal feeding components indicative of consistent/inconsistent eaters (Bus et al., 2023a), however, related to some of the day-level feeding components. During the first half of the growing-finishing phase, slower eaters and nibblers were more likely to eat at similar times from day to day. For the highest probability to eat, this could be an artefact of how day-to-day consistency was calculated, as pigs that eat more frequently are by definition more likely to eat at similar moments. However, this artefact is unlikely for the strength of the circadian rhythm, as this quantifies consistency across longer time frames. Instead, this suggests that pigs eating in larger meals eat at different moments from day to day, while pigs that nibble eat at similar

times each day. The moderate relationship between rate and the highest probability to eat additionally suggests that these consistent nibblers ate somewhat slower at younger ages. Across age, groups of pigs shift from nibbling to meal eating (Bigelow and Houpt, 1988; Boumans et al., 2015), eat faster (Boumans et al., 2015) and become more consistent in their timing of feeding (Bus et al., 2023a), which may reduce differences between pigs and explain the weakening of the correlation across the growing-finishing phase. We conclude that pigs show individual feeding strategies in the dimensions meal eating/nibbling, fast/slow eating, day/day-night feeding and consistent/inconsistent eating, with all dimensions but day/day-night feeding partially overlapping. At older ages, the dimensions become more independent of each other. These strategies should not be seen as clusters of pigs, but rather as a continuum along which pigs differ gradually.

4.2. Relationships to physical and behavioural characteristics

Heavier and faster-growing pigs had a higher rate and meal intake, corresponding to the previously-described reduction in these components' ICCs when final body weight was added to the model. No other relationships between physical characteristics and feeding components were identified. This suggests that body weight, whether it is expressed absolutely, as growth or relative to pen mates' body weight, has little influence on most aspects of individual feeding strategies. Rather, the relationship appears to be purely physical, where heavier pigs eat faster and more at each meal due to their larger oral and stomach capacities. Although similar results have been reported before (Gonyou and Lou, 2000), previous studies also reported that heavier pigs obtained less intake at night (Georgsson and Svendsen, 2002), which contradicts with

our results. These authors theorised that heavier pigs were more dominant and hence could feed more easily during the day when occupation levels were high (Georgsson and Svendsen, 2002). Therefore, an alternative explanation for heavier pigs commonly being meal eaters could be that they may have a higher dominance rank, making displacement from the feeder unlikely and thus facilitating eating in larger meals. However, we found only few indications that pigs displaying different social behaviours showed specific individual feeding strategies.

In our study, nibblers were more often displaced from the EFS, in line with previous studies showing that subordinate pigs used or were forced to use the nibbling strategy (Hoy et al., 2012; Ragab et al., 2019). Additionally, pigs with a lower rate were more often displaced from the EFS and subjected to aggression, which may indicate that slower-feeding pigs – who are likely the lighter pigs – are more subordinate. Pigs eating more consistently from day to day displaced pen mates from the EFS less often in month 3, possibly indicating that these were the subordinate pigs. Although this corresponds with the observed correlation between meal eating/nibbling and consistent/inconsistent eating, it contradicts our expectation that dominant pigs would be more consistent than subordinate pigs as they would have an easier time accessing the feeder (Bus et al., 2023a). Possibly, the most dominant pigs may never have had to displace a pen mate, as subordinate pigs may have avoided the feeder during times they knew dominant pigs would feed, and were thus not necessarily the inconsistent ones. In addition, pig ability to displace a pen mate is influenced by dominance as well as hunger (Arnott and Elwood, 2008) and may indicate little once the social structure in the group has stabilised, so it is unlikely to give the full picture.

Besides dominance, an alternative explanation for these relationships could be that the consistent nibblers were not necessarily subordinate but rather more active. Supporting this, we observed a tendency for an association between nibbling and initiating displacements from the feeder. If both displacing and being displaced are more frequent for the same individuals, this could suggest that increased feeder displacement is a result of eating during competitive hours, rather than of being subordinate. Indeed, many associations between pig activity and individual feeding strategies were identified. In general, nibblers and slow eaters came forward as the more active pigs. It could therefore be that heavier, fast-growing pigs were simply less active, spending less time standing up and exploring and minimising the time standing in the feeder. Additionally, more active pigs were also more consistent in their feeding than the less active pigs, aligning to the observed association between meal eating/nibbling and consistent/inconsistent eating. Activity could hence explain the underlying difference between meal eaters/nibblers as well as fast/slow eaters, rather than dominance, or a combination of activity and dominance where subordinate pigs tend to be more active.

Pig activity was also associated with feeding strategies via diurnal differences. Aligning with previous work at group level (Ingram et al., 1980), individual pigs that ate more at night tended to be more active during the night. As activity is a prerequisite for feeding, this association may hold little biological relevance. More inconsistent pigs, however, were less active during the day and both faster-eating and more inconsistent pigs were more inactive during peak activity hours, which cannot be explained by such a prerequisite. Instead, it suggests that these pigs, which were also the heavier pigs, were active when their pen mates were relatively inactive. This could indicate a personal preference in diurnal activity, similar to the well-recognised ‘chronotypes’ in humans (Bauducco et al., 2020; Druiven et al., 2021).

Some of the behaviours that we observed, such as play (Ahloy-Dal-laire et al., 2018; Boissy et al., 2007), social interactions (Boissy et al., 2007) and tail postures and movements (Camerlink and Ursinus, 2020), have been suggested as indicators of positive or negative emotions. A higher frequency of these behaviours could point towards a more positive or negative location on the affect balance and hence welfare (Reimert et al., 2023), which would relate certain feeding strategies with positive or negative welfare. We found, however, only few relationships

between these behaviours and feeding strategies, suggesting that basal feeding behaviour is not linked to pigs’ emotional states. Moreover, for the few identified relationships, simpler explanations are available. For example, the relationship between more nose-body contact and faster eating could be due to the higher inactivity of faster-eating pigs during peak activity hours, which would limit their opportunities for nose-body contact during the observation hours. Similarly, the relationship between more tail and ear manipulation and a higher consistency in feeding could be related to the general higher activity in more consistent pigs, as more active pigs may manipulate their pen mates more (Bagaria et al., 2022). Nevertheless, many of these behaviours were infrequent (Supplementary Table S6) and associations should be interpreted carefully.

4.3. Study limitations and suggestions for future research

The ICC is a group-level measure of behavioural repeatability. A high ICC shows that individuals within the population differ from each other in a relatively consistent way over time. Nevertheless, some individuals may be more consistent over time than others, and thus might adhere to a feeding strategy more or less strongly (Bell et al., 2009). With individual feeding strategies having been identified at group level, it would be interesting to see how they translate to the pig level. In addition, other aspects of the feeding strategies could be assessed, such as behavioural plasticity and predictability (Hertel et al., 2020), as pigs may develop their feeding strategies differently as they age or may be more or less persistent in their preferred strategies when their environment changes.

In this discussion, associations between feeding components and behavioural characteristics were mainly interpreted as if the behavioural variables reflect pig (personality) traits, i.e. as individual behavioural differences that are consistent across time and contexts (O’Malley et al., 2019). In support of this, activity, exploration, aggressiveness, sociability and boldness have all been identified as axes of pig personality (Finkemeier et al., 2018; O’Malley et al., 2019). It could, however, also be theorised that our behavioural observations did not reliably reflect pig (personality) traits but rather identified shorter-lasting pig states. More formal personality tests could be applied to confirm the associations identified in this study.

This study was of an explorative nature and its results should be interpreted as such. The behavioural observations enrolled a relatively limited number of pigs (21–30 per month), which may have led to limitations with statistical power, while the large number of models fitted increased the chances of false positive results. We mediated these limitations by selecting pigs for diversity in their feeding strategies and by applying P-value correction, yet despite these actions individual results should be interpreted carefully. In addition, many environmental factors can influence feeding behaviour, including but not limited to feed(er) type (Bergstrom et al., 2012), lighting regime (Ingram et al., 1980), and group size (Hyun and Ellis, 2002). As this study was performed in one barn with standardised housing and varying enrichment, results should be extrapolated to other housing systems with caution. It would be an interesting avenue for future research to expand these observations to other housing and management systems and types of pigs (e.g. breeds), where especially the type of feeding station used seems relevant.

Our study highlights interesting directions for further research into the understanding and use of individual feeding patterns. The existence of individual strategies in almost all feeding components suggests that these strategies must at least be corrected for when researching pig feeding behaviour. For example, data from EFSs are increasingly used to detect deviations in feeding behaviour that may be indicative of disease (e.g. Brown-Brandl et al., 2016; De Bruijn et al., 2023; Kaviak et al., 2023; Maselyne et al., 2018). The presence of individual feeding strategies, however, suggests that we cannot apply the same thresholds for ‘deviant’ behaviour to each pig, nor can we easily identify the effect of a

disease on feeding behaviour by comparing pigs against each other, as pigs may have different basal feeding strategies. Therefore, alternative detection methods must be developed.

5. Conclusion

We conclude that individual feeding strategies of growing-finishing pigs exist along continua in four dimensions: 1) nibbling vs. meal eating, 2) fast vs. slow eating, 3) day vs. day and night eating, and 4) consistent vs. inconsistent eating from day to day. These feeding strategies were sustained after correction for sex and body weight, or were not influenced by such correction at all. Especially at younger ages, the dimensions of nibbling/meal eating, fast/slow eating, and consistent/inconsistent eating partially overlapped. Pigs with different feeding strategies differed in their general activity, diurnal activity and possibly dominance. We saw that heavier (and possibly more dominant pigs) were more likely to eat in meals and eat inconsistently from day-to-day, and that these more inconsistent meal eaters were also less active across the day and during the peak hours of activity. We found no indications that the individual feeding strategies of pigs related to behaviours possibly indicative of positive or negative emotional states. Our results suggest that individual differences in the feeding behaviour of pigs must be taken into account when studying pig feeding patterns.

CRedit authorship contribution statement

Jacinta D. Bus: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft. **Iris J.M.M. Boumans:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing. **Dennis E. te Beest:** Formal analysis, Methodology, Writing – review & editing. **Laura E. Webb:** Conceptualization, Methodology, Supervision, Writing – review & editing. **J. Elizabeth Bolhuis:** Conceptualization, Methodology, Writing – review & editing. **Eddie A.M. Bokkers:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.applanim.2024.106208](https://doi.org/10.1016/j.applanim.2024.106208).

References

- Ahloy-Dallaire, J., Espinosa, J., Mason, G., 2018. Play and optimal welfare: does play indicate the presence of positive affective states? *Behav. Process.* 156, 3–15. <https://doi.org/10.1016/j.beproc.2017.11.011>.
- Arnott, G., Elwood, R.W., 2008. Information gathering and decision making about resource value in animal contests. *Anim. Behav.* 76, 529–542. <https://doi.org/10.1016/j.anbehav.2008.04.019>.
- Bagaria, M., Kuiper, L., Meijer, E., Sterck, E.H.M., 2022. Individual behavioral correlates of tail biting in pre-finishing piglets. *Front. Vet. Sci.* 9, 1–14. <https://doi.org/10.3389/fvets.2022.1033463>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bauducco, S., Richardson, C., Gradisar, M., 2020. Chronotype, circadian rhythms and mood. *Curr. Opin. Psychol.* 34, 77–83. <https://doi.org/10.1016/j.copsyc.2019.09.002>.
- Bell, A.M., Hankison, S.J., Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis. *Anim. Behav.* 77, 771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>.
- Bergstrom, J.R., Nelssen, J.L., Edwards, L.N., Tokach, M.D., Dritz, S.S., Goodband, R.D., Derouchey, J.M., 2012. Effects of feeder design and changing source of water to a location separate from the wet-dry feeder at 4 or 8 weeks before harvest on growth, feeding behavior, and carcass characteristics of finishing pigs. *J. Anim. Sci.* 90, 4567–4575. <https://doi.org/10.2527/jas.2011-4486>.
- Bigelow, J.A., Houpt, T.R., 1988. Feeding and drinking patterns in young pigs. *Physiol. Behav.* 43, 99–109. [https://doi.org/10.1016/0031-9384\(88\)90104-7](https://doi.org/10.1016/0031-9384(88)90104-7).
- Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., Aubert, A., 2007. Assessment of positive emotions in animals to improve their welfare. *Physiol. Behav.* 92, 375–397. <https://doi.org/10.1016/j.physbeh.2007.02.003>.
- Boumans, I.J.M.M., Bokkers, E.A.M., Hofstede, G.J., De Boer, I.J.M., 2015. Understanding feeding patterns in growing pigs by modelling growth and motivation. *Appl. Anim. Behav. Sci.* 171, 69–80. <https://doi.org/10.1016/j.applanim.2015.08.013>.
- Boumans, I.J.M.M., De Boer, I.J.M., Hofstede, G.J., Bokkers, E.A.M., 2018a. How social factors and behavioural strategies affect feeding and social interaction patterns in pigs. *Physiol. Behav.* 194, 23–40. <https://doi.org/10.1016/j.physbeh.2018.04.032>.
- Boumans, I.J.M.M., De Boer, I.J.M., Hofstede, G.J., Bokkers, E.A.M., 2018b. Unravelling variation in feeding, social interaction and growth patterns among pigs using an agent-based model. *Physiol. Behav.* 191, 100–115. <https://doi.org/10.1016/j.physbeh.2018.03.030>.
- Brooks, M.E., Kristensen, K., Benthem, K.J., van, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400. <https://doi.org/10.3929/ethz-b-000240890>.
- Brown-Brandl, T.M., Jones, D.D., Eigenberg, R.A., 2016. Modeling feeding behavior of swine to detect illness, in: CIGR-AgEng Conference. pp. 1–6.
- Bus, J.D., Boumans, I.J.M.M., Engel, J., Beest, D.E., te Webb, L.E., Bokkers, E.A.M., 2023a. Circadian rhythms and diurnal patterns in the feed intake behaviour of growing-finishing pigs. *Sci. Rep.* 13, 16021. <https://doi.org/10.1038/s41598-023-42612-1>.
- Bus, J.D., Boumans, I.J.M.M., Stauble, L., Webb, L.E., Bokkers, E.A.M., 2023b. A critical note on meal criteria in growing-finishing pigs: Behaviour between feeder visits. *Book Abstr. 56th Congr. Int. Soc. Appl. Ethol.* 15.
- Bus, J.D., Boumans, I.J.M.M., Webb, L.E., Bokkers, E.A.M., 2021. The potential of feeding patterns to assess generic welfare in growing-finishing pigs. *Appl. Anim. Behav. Sci.* 241, 17. <https://doi.org/10.1016/j.applanim.2021.105383>.
- Bus, J.D., Walderveen, A., van, Bolhuis, J.E., Boumans, I.J.M.M., Bokkers, E.A.M., 2023c. Protocol for health observations in growing-finishing pigs. *DANS*. <https://doi.org/10.17026/dans-xt2-xpej>.
- Camerlink, I., Ursinus, W.W., 2020. Tail postures and tail motion in pigs: a review. *Appl. Anim. Behav. Sci.* 230, 9. <https://doi.org/10.1016/j.applanim.2020.105079>.
- Casey, D.S., Stern, H.S., Dekkers, J.C.M., 2005. Identification of errors and factors associated with errors in data from electronic swine feeders. *J. Anim. Sci.* 83, 969–982. <https://doi.org/10.2527/2005.835969x>.
- De Bruijn, B.G.C., De Mol, R.M., Hogewerf, P.H., Van Der Fels, J.B., 2023. A correlated-variables model for monitoring individual growing-finishing pig's behavior by RFID registrations. *Smart Agric. Technol. Prepr.* <https://doi.org/10.1016/j.atech.2023.100189>.
- Druiven, S.J.M., Riese, H., Kamphuis, J., Haarman, B.C.M., Antypa, N., Penninx, B.W.J.H., Schoevers, R.A., Meesters, Y., 2021. Chronotype changes with age; seven-year follow-up from the Netherlands study of depression and anxiety cohort. *J. Affect. Disord.* 295, 1118–1121. <https://doi.org/10.1016/j.jad.2021.08.095>.
- Eissen, J.J., Kanis, E., Merks, J.W.M., 1998. Algorithms for identifying errors in individual feed intake data of growing pigs in group-housing. *Appl. Eng. Agric.* 14, 667–673. <https://doi.org/10.13031/2013.19421>.
- Fàbrega, E., Velarde, A., Cros, J., Gispert, M., Suárez, P., Tibau, J., Soler, J., 2010. Effect of vaccination against gonadotrophin-releasing hormone, using improvac®, on growth performance, body composition, behaviour and acute phase proteins. *Livest. Sci.* 132, 53–59. <https://doi.org/10.1016/j.livsci.2010.04.021>.
- Fernández, J., Fàbrega, E., Soler, J., Tibau, J., Ruiz, J.L., Puigvert, X., Manteca, X., 2011. Feeding strategy in group-housed growing pigs of four different breeds. *Appl. Anim. Behav. Sci.* 134, 109–120. <https://doi.org/10.1016/j.applanim.2011.06.018>.
- Finkemeier, M.A., Langbein, J., Puppe, B., 2018. Personality research in mammalian farm animals: concepts, measures, and relationship to welfare. *Front. Vet. Sci.* 5. <https://doi.org/10.3389/fvets.2018.00131>.

- Fox, J., Weisberg, S., 2019. An R companion to applied regression, 3rd ed. Sage Publications.
- Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* 7, 1325–1330. <https://doi.org/10.1111/2041-210X.12584>.
- Garrido-Izard, M., Correa, E.C., Requejo, J.M., Diezma, B., 2020. Continuous monitoring of pigs in fattening using a multi-sensor system: behavior patterns. *Animals* 10, 17. <https://doi.org/10.3390/ani10010052>.
- Gelman, A., Su, Y., 2022. Arm: Data analysis using regression and multilevel/hierarchical models.
- Georgsson, L., Svendsen, J., 2002. Degree of competition at feeding differentially affects behavior and performance of group-housed growing-finishing pigs of different relative weights. *J. Anim. Sci.* 80, 376–383. <https://doi.org/10.2527/2002.802376x>.
- Gohel, D., Skintzos, P., 2023. Flextable: Functions for tabular reporting.
- Gonyou, H.W., Lou, Z., 2000. Effects of eating space and availability of water in feeders on productivity and eating behavior of grower/finisher pigs. *J. Anim. Sci.* 78, 865–870. <https://doi.org/10.2527/2000.784865x>.
- Harrell Jr, F.E., 2023. Hmisc: Harrell miscellaneous.
- Helm, E.T., Outhouse, A.C., Schwartz, K.J., Dekkers, J.C.M., Lonergan, S.M., Rauw, W. M., Gabler, N.K., 2018a. Impact of mycoplasma hyopneumoniae and lawsonia intracellularis on the performance of pigs divergently selected for feed efficiency. *J. Anim. Sci.* 96, 462–472. <https://doi.org/10.1093/jas/skx074>.
- Helm, E.T., Outhouse, A.C., Schwartz, K.J., Lonergan, S.M., Curry, S.M., Dekkers, J.C.M., Gabler, N.K., 2018b. Metabolic adaptation of pigs to a mycoplasma hyopneumoniae and lawsonia intracellularis dual challenge. *J. Anim. Sci.* 96, 3196–3207. <https://doi.org/10.1093/jas/sky220>.
- Hertel, A.G., Niemelä, P.T., Dingemans, N.J., Mueller, T., 2020. A guide for studying among-individual behavioral variation from movement data in the wild. *Mov. Ecol.* 8 <https://doi.org/10.1186/s40462-020-00216-8>.
- Hoy, S., Schamun, S., Weirich, C., 2012. Investigations on feed intake and social behaviour of fattening pigs fed at an electronic feeding station. *Appl. Anim. Behav. Sci.* 139, 58–64. <https://doi.org/10.1016/j.applanim.2012.03.010>.
- Hyun, Y., Ellis, M., 2002. Effect of group size and feeder type on growth performance and feeding patterns in finishing pigs. *J. Anim. Sci.* 80, 568–574. <https://doi.org/10.2527/2002.803568x>.
- Ingram, D.L., Walters, D.E., Legge, K.F., 1980. Variations in motor activity and in food and water intake over 24h periods in pigs. *J. Agric. Sci.* 95, 371–380. <https://doi.org/10.1017/S002185960003940X>.
- Kavlak, A.T., Pastell, M., Uimari, P., 2023. Disease detection in pigs based on feeding behaviour traits using machine learning. *Biosyst. Eng.* 226, 132–143. <https://doi.org/10.1016/j.biosystemseng.2023.01.004>.
- Knap, P., 2009. Voluntary feed intake and pig breeding. *Volunt. Feed intake pigs*. <https://doi.org/10.3920/978-90-8686-689-2>.
- Labroue, F., Guéblez, R., Sellier, P., 1997. Genetic parameters of feeding behaviour and performance traits in group-housed large white and french landrace growing pigs. *Genet. Sel. Evol.* 29, 451–468. <https://doi.org/10.1051/gse:19970403>.
- Labroue, F., Guéblez, R., Sellier, P., Meunier-Salaün, M.C., 1994. Feeding behaviour of group-housed large white and landrace pigs in french central test stations. *Livest. Prod. Sci.* 40, 303–312. [https://doi.org/10.1016/0301-6226\(94\)90097-3](https://doi.org/10.1016/0301-6226(94)90097-3).
- Leiber-Schotte, C., 2009. Einfluss der rangordnung bei jungen im eigenleistungstest auf futteraufnahme und futteraufnahmeverhalten unter berücksichtigung endokrinologischer und immunologischer parameter. Christian-Albrechts-Universität zu Kiel.
- Lenth, R.V., 2022. Emmeans: Estimated marginal means, aka least-squares means.
- Maselyne, J., Saews, W., Van Nuffel, A., 2015. Review: quantifying animal feeding behaviour with a focus on pigs. *Physiol. Behav.* 138, 37–51. <https://doi.org/10.1016/j.physbeh.2014.09.012>.
- Maselyne, J., Van Nuffel, A., Briene, P., Vangeyete, J., De Ketelaere, B., Millet, S., Van den Hof, J., Maes, D., Saews, W., 2018. Online warning systems for individual fattening pigs based on their feeding pattern. *Biosyst. Eng.* 173, 143–156. <https://doi.org/10.1016/j.biosystemseng.2017.08.006>.
- Morrow, A.T.S., Walker, N., 1994. Effects of number and siting of single-space feeders on performance and feeding behaviour of growing pigs. *J. Agric. Sci.* 122, 465–470. <https://doi.org/10.1017/S002185960006740X>.
- Munsterhjelm, C., Nordgreen, J., Aae, F., Heinonen, M., Olstad, K., Aasmundstad, T., Janczak, A.M., Valros, A., 2017. To be blamed or pitied? The effect of illness on social behavior, cytokine levels and feed intake in unlocked boars. *Physiol. Behav.* 179, 298–307. <https://doi.org/10.1016/j.physbeh.2017.06.024>.
- Nielsen, B.L., 1999. On the interpretation of feeding behaviour measures and the use of feeding rate as an indicator of social constraint. *Appl. Anim. Behav. Sci.* 63, 79–91. [https://doi.org/10.1016/S0168-1591\(99\)00003-9](https://doi.org/10.1016/S0168-1591(99)00003-9).
- O'Malley, C.I., Turner, S.P., D'Eath, R.B., Steibel, J.P., Bates, R.O., Ernst, C.W., Siegford, J.M., 2019. Animal personality in the management and welfare of pigs. *Appl. Anim. Behav. Sci.* 218, 17. <https://doi.org/10.1016/j.applanim.2019.06.002>.
- Quiniou, N., Dubois, S., Noblet, J., 2000. Voluntary feed intake and feeding behaviour of group-housed growing pigs are affected by ambient temperature and body weight. *Livest. Prod. Sci.* 63, 245–253. [https://doi.org/10.1016/S0301-6226\(99\)00135-9](https://doi.org/10.1016/S0301-6226(99)00135-9).
- R Core Team, 2023. R: A language and environment for statistical computing.
- Ragab, M., Piles, M., Quintanilla, R., Sánchez, J.P., 2019. Indirect genetic effect model using feeding behaviour traits to define the degree of interaction between mates: An implementation in pigs growth rate. *Animal* 13, 231–239. <https://doi.org/10.1017/S1751731118001192>.
- Reimert, I., Webb, L.E., Marwijk, M.A., van, Bolhuis, J.E., 2023. Review: Towards an integrated concept of animal welfare. *Animal In press*. <https://doi.org/10.1016/j.animal.2023.100838>.
- Rigby, R.A., Stasinopoulos, D.M., 2005. Generalized additive models for location, scale and shape. *Discuss. J. Appl. Stat.* 54, 507–554. <https://doi.org/10.1111/j.1467-9876.2005.00510.x>.
- Roesch, A., Schmidbauer, H., 2018. WaveletComp: Computational wavelet analysis.
- Schmidt, T., Calabrese, J.M., Grodzycy, M., Paulick, M., Pearce, M.C., Rau, F., Von Borell, E., 2011. Impact of single-sex and mixed-sex group housing of boars vaccinated against GnRF or physically castrated on body lesions, feeding behaviour and weight gain. *Appl. Anim. Behav. Sci.* 130, 42–52. <https://doi.org/10.1016/j.applanim.2010.11.019>.
- Schweer, W., Schwartz, K., Burrough, E., Yoon, K., Sparks, J., Gabler, N., 2016. The effect of porcine reproductive and respiratory syndrome virus and porcine epidemic diarrhoea virus challenge on growing pigs i: growth performance and digestibility. *J. Anim. Sci.* 94, 514–522. <https://doi.org/10.2527/jas2015-9834>.
- Tolkamp, B.J., Allcroft, D.J., Austin, E.J., Nielsen, B.L., Kyriazakis, I., 1998. Satiety splits feeding behaviour into bouts. *J. Theor. Biol.* 194, 235–250. <https://doi.org/10.1006/jtbi.1998.0759>.
- Tolkamp, B.J., Schweitzer, D.P.N., Kyriazakis, I., 2000. The biologically relevant unit for the analysis of short-term feeding behavior of dairy cows. *J. Dairy Sci.* 83, 2057–2068. [https://doi.org/10.3168/jds.S0022-0302\(00\)75087-9](https://doi.org/10.3168/jds.S0022-0302(00)75087-9).
- Wickham, H., 2016. ggplot2: Elegant graphics for data analysis, 2nd ed. Springer-Verlag. <https://doi.org/10.1007/978-3-319-24277-4>.
- Yeates, M.P., Tolkamp, B.J., Allcroft, D.J., Kyriazakis, I., 2001. The use of mixed distribution models to determine bout criteria for analysis of animal behaviour. *J. Theor. Biol.* 213, 413–425. <https://doi.org/10.1006/jtbi.2001.2425>.