Applied Animal Behaviour Science 259 (2023) 105836

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

Play behaviour positively relates to weight gain, feeding behaviour and drinking behaviour in weaner pigs (*Sus scrofa*)

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ARTICLE INFO

Keywords:
Positive animal welfare
Locomotor-rotational play
Social play
Early weaning
Growth
Hunger

ABSTRACT

Engagement in play behaviour has been associated with the presence of positive affective states and, thus, proposed to be an indicator of positive animal welfare. However, the interpretation of play in animals remains challenging due to the complexity of motivating factors. Accordingly, we aimed to clarify whether Yorkshire × Landrace weaner pigs would engage more in play behaviour the more well-nourished they were by examining the effects of weight gain, feeding behaviour, and drinking behaviour on two types of play behaviour [locomotor-rotational play (LOC) and social play (SOC)]. In total, 24 litters [pigs/litter: (mean ± SD) 13 ± 2] raised under conventional husbandry conditions were included in this study. Each pig was manually weighed within 24 h of birth and on days − 7, 0, 1, 2 relative to the weaning day (day 0) at approximately 26 days of age. All behavioural measures were registered via video at individual level. Visits to feeder and drinker were registered from 07:00 h to 21:59 h on days − 1 and 1 using 2-min interval instantaneous sampling. The proportion of visits to each resource was calculated by dividing the number of scans visiting the resource by the total number of daily scans. The latencies to visit the feeder and drinker within the first 24 h post-weaning were continuously recorded. Both LOC and SOC were registered between 14:00 h and 22:00 h on days − 1, 1 and 2. Both before and after weaning, heavier pigs spent more time performing LOC. Before weaning, heavier pigs spent more time performing SOC. Proportion of visits to the feeder positively related to LOC after weaning. On the day before weaning, the proportion of visits to the drinker positively related to LOC. No clear relationships between the latency to feed and drink after weaning and play behaviour were found. Our study supports the hypothesis that motivation to play is higher when animals are in more stable conditions, e.g., well-nourished, and healthier than under suboptimal conditions. However, the fact that the nutritional measures did not similarly affect LOC and SOC suggests that these two types of play behaviour may be differently affected by the weaning context and questions whether they have the same underlying motivation. This study represents a step toward the validation of play as a positive animal welfare indicator.

1. Introduction

The performance of play behaviour occurs during the physical, physiological, and psychological development of mammals (Siviy, 1998; Špinka et al., 2001). Prior work reported that juvenile mammals typically perform this behaviour when their primary needs, such as food and safety, have been met (Newberry et al., 1988; Špinka et al., 2001; Held and Špinka, 2011). Conversely, a low or no engagement in play behaviour in juveniles suggests the presence of physical, physiological, or psychological challenges (Burghardt, 2005; Burgdorf and Panksepp, 2007). In fact, play behaviour is considered an energetically and cognitively demanding activity that is displayed in a relatively safe and stable environment (Špinka et al., 2001). Furthermore, the performance of play behaviour is thought to be reinforcing and associated with positive affective states (Burghardt, 2005). With the increasing concern that the welfare of animals should be safeguarded by not only avoiding the experience of negative affective states, but also promoting the experience of positive ones, play behaviour has been suggested as a potential

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https://doi.org/10.1016/j.applanim.2023.105836
Received 25 October 2022; Received in revised form 11 January 2023; Accepted 16 January 2023
Available online 17 January 2023

positive animal welfare indicator (Boissy et al., 2007; Yeates and Main, 2008).

Undernourishment and hunger are acknowledged to negatively impact animal welfare and to limit the performance of play behaviour (Špinka et al., 2001; Boissy et al., 2007). For instance, in dairy calves, low milk allowance (Duve et al., 2012; Jensen et al., 2015) and premature weaning (Miguel-Pacheco et al., 2015; Rushen et al., 2016) induced a decrease in locomotor play duration. Similarly, earlier studies reported a reduction in social play duration in undernourished wild animals (e.g., Hanuman langurs (*Presbytis entellus*) – Sommer and Mendoza-Granados, 1995; primates – Loy, 1970; wild meerkats (*Suricata suricatta*) – Sharpe et al., 2002). On the contrary, food rationing reportedly led to an increase in object play duration in domestic kittens (*Felis cattus*) (Bateson et al., 1990; Hall and Bradshaw, 1998) and social play duration in juvenile rats (*Rattus norvegicus*) (Loranca et al., 1999). In the kittens' example, object play may be motivated similarly to predatory behaviour, which can be stimulated when food availability is limited. In the rats' example, social play may be difficult to distinguish from agonistic interactions. Furthermore, for both kittens and juvenile rats, the authors speculated that those young animals interpreted the reduced food supply as a cue to accelerate their development and engagement in play behaviour while it was still feasible. These contrasting findings illustrate the complexity of play behaviour and underline the need for studies assessing the validity of various types of play behaviour as positive animal welfare indicators against other validated welfare measures (Martin and Caro, 1985; Špinka et al., 2001; Ahloy-Dallaire et al., 2018).

In a natural setting, the period the sow nurses her offspring gradually declines from approximately 10 days post-partum (pp) and by 4–5 months of age nursing ends and pigs become fully habituated to solid feed (Jensen and Stangel, 1992). In contrast, pigs raised in modern production systems are abruptly weaned from their sow and shift from milk to solid feed at approximately 3–5 weeks of age (Špinka, 2017). Hence, weaning is a management practice known to inflict nutritional stress in pigs (Donaldson et al., 2002; Weary et al., 2008) and constitutes a suitable context for the examination of the validity of play behaviour as an animal welfare indicator. Accordingly, our study explored the effects of weight gain, feeding behaviour (i.e., visits to feeder before and after weaning and latency to visit the feeder after weaning) and drinking behaviour (i.e., visits to drinker before and after weaning and latency to visit the drinker after weaning) on two types of play behaviour (locomotor-rotational and social play in weaner pigs. Before and after weaning, we hypothesised that pigs with higher weight gain and displaying higher frequency of visits to the feeder and drinker, signalling better nourishment, would show a higher engagement with play behaviour.

2. Materials and methods

This study took place from February to November 2020 at the experimental facilities at the Department of Animal and Veterinary Sciences, Aarhus University, Viborg, Denmark. The experimental procedures were carried out in accordance with the Ministry of Food, Agriculture and Fisheries, The Danish Veterinary and Food Administration under act 474 of 15. May 2014 and executive order 2028 of 14. December 2020, and under consideration of the ARRIVE Guidelines (Du Sert et al., 2020). The present study is part of a large study examining the clinical, physiological, and behavioural effects of weaning intact litters in farrowing pens for loose-housed sows and sow hybrid featured by reduced litter size and pigs with increased individual birth and weaning weight described in detail by Franchi et al., (2022b) and Winters et al. (2022).

2.1. Animals, housing, and management

Six DanBred Landrace × Yorkshire (DB) gilts and six Topigs Norsvin TN-70 Yorkshire × Landrace (TN) gilts were included in one batch. Following farrowing, the twelve sows returned in a second batch as second-parity sows. Both genetic hybrids were inseminated with semen of DanBred Duroc boars. A total of 306 pigs (50% castrated males, 50% females) from 24 litters (pigs/litter: (mean ± SD) 13 ± 2; birth weight: 1.4 ± 0.3 kg (both DB and TN)) across both batches were studied. The farrowing unit had two sections, each containing eight 3.0 × 2.2 m farrowing pens for loose-housed sows (FT30, Jyden A/S, Denmark; approximately 0.51 m^2/pig). Each pen had 41% slatted-flooring and 59% solid-concrete-flooring (heated) and was equipped with sloped walls to reduce the risk of pig crushing by the sow, a 0.9 m^2 hayrack next to the covered pig creep area (0.9 m^2; equipped with a 150 W infrared heat lamp), a low 80 × 28 cm polyconcrete feeder (Jyden A/S, Denmark; Fig. 1A) filled with sow lactation diet (Die Profil Lac, DLG, Denmark, 15.6% crude protein) allowing pigs to eat together with the sow, and a 31 × 17 × 11 cm pig drinker (Aqua-Level system with hinged trough, Jyden A/S, Denmark; Fig. 1A) allowing pigs to drink with the sow. The artificial light was on from 07:00 h to 21:59 h. Every morning, feeders were emptied before first feeding and manure was removed. Straw racks were filled with wheat straw daily and approximately 130 g of fine chopped wheat straw were provided on the solid floor daily. Approximately 400 g of sawdust were provided in the pig creep area daily. At farrowing, the room temperature was set at 21 °C and gradually decreased to 19 °C at weaning. Sows received analgesic (Metacam®) at farrowing and all pigs were weighed, ear tagged and had their umbilical cord cut following farrowing (if it ended before 15:00 h) or on the next morning (if farrowing ended after 15:00 h). The number of own pigs nursed by the sows was equalised to the number of functional teats. Surplus pigs within sow hybrid were cross fostered within the first 3 days pp to sows that had fewer pigs than functional teats. If no sows were available for cross fostering, surplus pigs were euthanised by blunt force trauma. Non-viable pigs and pigs below 700 g were euthanised first followed by randomly selected pigs. On day − 1 relative to weaning, the number of pigs per pen in the DB and TN genetic hybrids were 12 ± 2 and 13 ± 2, respectively. No pigs were tail-docked or tooth-clipped.

On the day of weaning, experimental pigs were (mean ± SD) 26 ± 1 days old and weighing 7.4 ± 1.9 kg (DB: 7.0 ± 2.0 kg; TN: 7.8 ± 1.8 kg). At weaning, the sow was removed out of sensory range of the pigs. To accommodate all-in all-out farrowing for hygiene purposes, weaning took place on one day per week, as close as possible to the day when litters were 28 days old. In each batch, 1/3 of the DB and TN litters stayed in the farrowing pen as an intact litter after weaning (13 ± 2 pigs/pen) and the other 2/3 were moved and mixed with another litter in one of four identical 5.40 × 2.45 m two-climate weaner pens (26 ± 2 pigs/pen; approximately 0.51 m^2/pig) with approximately 67% slatted and 33% solid floor in the same weaner unit. The solid floor area was roofed by a manually adjustable fibre panel positioned approximately 85 cm above the floor level (Jyden A/S, Denmark) providing two zones in the pen (a cooler slatted and drained floor area and a warmer and darker area under the roof). The drinker was the same type as the one used in the farrowing pens. Two identical weaner feeders (TR4, Rotecna®, Spain; Fig. 1B) were placed next to each other in the partially slatted floor area, providing eight 14 × 18 cm feeding places per weaner pen. In both locations (farrowing pen and two-climate weaner pen), the pigs were ad libitum fed a pelleted standardised weaner diet (Prime Midi Piller, DLG, Denmark, metabolizable energy: 14.8 MJ/kg, 19.3% crude protein), with no medical zinc oxide added to it, delivered once daily in the morning. The room temperature was increased to 24 °C and gradually decreased to 21 °C 56 days post-weaning. At the time of weaning and every morning post-weaning, all farrowing pens received approximately 130 g of chopped wheat straw on the solid floor and approximately 400 g of sawdust in the creep area. The two-climate weaner pens received double the amount of straw and sawdust (to maintain same provision per animal) placed on the partly slatted floor and on the solid floor, respectively.

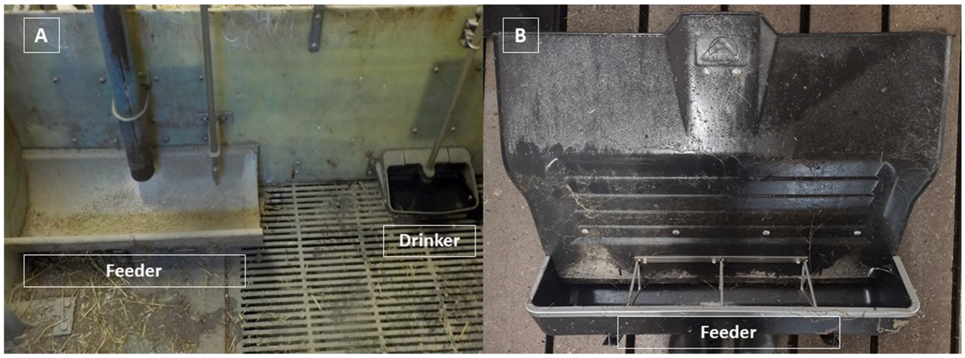

Fig. 1. Illustration of the feeders and drinker installed in the farrowing pen (subfigure A) and weaner pen (subfigure B). Both farrowing and two-climate weaner pens were equipped with similar drinkers.

2.2. Clinical recording

All pigs were individually weighed within 24 h of birth and on days − 7, 0, 1, and 2, between 08:00 h and 12:00 h, relative to the day of weaning. Pig weight gain in the pre-weaning period (i.e., from birth to weaning, from day −7 to weaning) and post-weaning period (i.e., from weaning to day 1, from weaning to day 2, and from day 1 to day 2) was calculated as end period weight minus start period weight and divided by the number of days. Weight gain is presented in grams per day (g/d).

2.3. Behaviour recording

A 2D video camera (model DS-2CD2145FWD-I, Hikvision, China) was placed above each pen with a top-view angle, overlooking the entire pen area, except under the creep area in the farrowing pen and under the cover in the climate pen, from a height of approximately 2.3 m in the farrowing pen and 2.8 m in the weaner pen. Video data were processed with the software Blue Iris v.5 (Blue Iris Security, USA). Each pig was identified on the video recordings by use of markings on the back made with a livestock marker on days − 2, 0, 1 and 2 at between 08:00 h and 12:00 h.

2.3.1. Play behaviour

Play behaviour was observed at individual level from video recordings on days − 1, 1 and 2 relative to weaning from 14:00 h to 22:00 h (i.e., period with least disturbance across pens and artificial light on) following behavioural sampling and continuous recording (Bateson and Martin, 2021) and using Noldus Observer XT 15 (Noldus Information Technology, The Netherlands) software package. The durations (s/pig/8-h period) of two types of play behaviour were recorded separately: locomotor-rotational play (LOC) and social play (SOC), according to the ethogram described in Table 1. The durations of LOC and SOC of the individual pig comprised the sum of durations per 8-h observation period of all behavioural elements constituting each type of play. Whenever pigs were disturbed (i.e., a human was within the framework of the pen, or the pigs were not in the pen, or the pigs were being moved in or out of the pen), this was noted, and no behavioural registrations were made. The duration of disturbance across pens ranged from 0 to 150 s on day − 1, 0–47 s on day 1 and 0–51 s on day 2. Three experimenters were assigned to register play behaviour from video recordings of the pigs, balanced for treatments (genetic hybrid × weaning method), and the inter-experimenter agreement on the total durations of LOC, SOC, and combination of LOC and SOC of the individual pig were assessed with Concordance Correlation Coefficient (CCC; Lawrence and Lin, 1989). Based on the criteria proposed by Hinkle et al. (2003), we interpreted CCC > 0.8 as high agreement level. The achieved CCC for LOC was 0.82; for SOC was 0.91; and for the combination of LOC and SOC was 0.82.

2.3.2. Feeding and drinking behaviour

Individual visits to feeder and drinker were registered on days − 1 and 1 using instantaneous sampling at 2-min intervals (Bateson and Martin, 2021) for a 13-h period from 07:00 h to 20:00 h (450 scans/-day). This sampling interval was chosen based on time availability and confirmed by a pilot study with 13 non-experimental pigs during 13 h on the day before weaning demonstrating the individual proportion of visits to feeder and drinker labelled instantaneously at 2-min interval highly agreed with the respective outcomes labelled continuously (nonparametric concordance test index = 0.96 (visits to feeder) and 0.89 (visits to drinker); Winters et al., unpublished data). Visits to each resource were defined as a pig having its head including both ears within the area of the feeder or drinker with its nose pointing downwards (Winters et al., 2022). The visits to feeder and drinker were observed by one trained experimenter and the order of observed pens was randomised across treatments, batches, and days to avoid systematic drift in the observation over time. Additionally, the individual latency to visit the feeder and drinker (i.e., the pig having its head and both ears above the edge of the trough with its nose pointing downward for minimum 5 s (feeder) or 2 s (drinker) (Winters et al., 2022)) within the first 24 h post-weaning was recorded continuously by two experimenters and the order of observed pens was randomised between treatments and batches. The time point was recorded to the nearest minute and a maximum latency of 1440 min (24 h) was used, after which latencies were right-censored. No intra- or inter-experimenter agreement calculations were performed for visit measurements or latency measurements.

2.4. Statistical analyses

Statistical analyses were performed in R v.2.1–461 (R Core Team, 2021) at individual level accounting for the nested structure in data with pigs nested in pens. P-values < 0.05 were considered significant, and values of 0.1 > P ≥ 0.05 were considered tendencies. The current manuscript focuses on the effects of measures of nutritional status on play. The effects of genetic hybrids and weaning methods on LOC and SOC are reported in Franchi et al., (2022b), while effects on the measures of nutritional status are reported in Winters et al. (2022). The effects of weight gain, proportion of visits to feeder (i.e., number of scans visiting the feeder divided by the maximum number of daily scans) and proportion of visits to drinker (i.e., number of scans visiting the drinker divided by the maximum number of daily scans) (independent variables) on LOC and SOC (dependent variables) were analysed with mixed-effects modelling (library *glmmTMB* v.1.1.2; Brooks et al., 2017) on each day (−1, 1 and 2) separately. The description of the models for each day relative to weaning is presented in Table 2. Each independent variable was transformed into a categorical variable on each day using the 33% and 67% quantiles (Table 2). On day − 1 (11% zero observations), LOC was square-root-transformed to fulfil the assumptions of

Table 1
Ethogram of behavioural elements constituting locomotor-rotational play (LOC) and social play (SOC) in domesticated pigs.

Play type	Behavioural element	Definition
LOC[a]	Gambolling	Gallop-like energetic running (the 2 forelimbs move approximately in phase, followed by the 2 hind limbs) and hopping in forward motions within the pen environment. Often associated with vigorous ear flapping, moving across a large area of the pen, and occasionally bouncing into other pigs. As part of a bout of gambolling, the pig may turn and change direction. The behaviour ends when the pigs move at a slower pace or go out of sight.
	Scamper	Performing at least 2 hops forward in rapid succession usually accompanied by ear flapping and sometimes accompanied by head tossing. The behaviour ends when the pigs move at a slower pace or go out of sight.
	Flop	A rapid drop from an upright position to sternal or lateral recumbency in which the pig appears to fall by itself and not because of contact with another pig.
	Head toss	Exaggerated lateral movement of the head and neck in the horizontal plane, involving at least 1 full movement to each side.
	Hop /Pivot	Making a short, bouncing leap on the spot during which all feet are simultaneously lifted off the ground, body oriented in the same direction throughout the hop or rotated rapidly in the horizontal plane.
	Turn	Rapid turning around the body axis on the spot during which at least one foot is touching the ground.
	Shake straw	Perform vigorous lateral movements of head and neck while holding straw, which protrudes from mouth.
	Throw straw	Holding straw in the mouth and throwing it through the air by a rapid movement of the head and neck.
SOC[b]	Climb	Placing both front hoofs on the back of another pig.
	Follow/chase	Walking/running (often with physical contact) in the same direction as another pig.
	Lever	With the snout lifting another pig so that at least two feet are lifted off the floor.
	Nudge	Use of snout to gently touch another pig's body, not including naso-naso contact.
	Push	Using head, neck, or shoulders with minimal or moderate force to drive into another pig's body.
	Play fight	Two pigs mutually push and head-knock each other. A general mild intensity of the performed fighting behaviours and a lack of biting or avoidance distinguish play fight from aggressive fighting.

[a] Behavioural elements are mutually exclusive and recorded with exact start and stop times. If the pig stops playing for a full second, it is noted as a new event.
[b] Energetic mutual interaction between two or more upright pigs initiated by play fighting. Pigs display neither biting nor avoidance. The social play ends when the pigs are no longer in contact, or when one pig no longer shows interest, or when they stop follow/chase, or if at least one of the pigs moves out of sight. Adapted from Franchi et al., (2022b)

Table 2
Description of independent variables' (weight gain, proportion of visits to feeder, proportion of visits to drinker) levels and random effects included in the models to examine the relationships between the independent variables and locomotor-rotational play and social play on each day relative to weaning (day 0). Each independent variable was transformed into categorical variable on each day using the 33% and 67% quantiles. Each row represents a different model.

Day	Independent variable	Covariate	Random effects
-1	Weight gain from birth to weaning day (low: ≤209 g/d, n = 99; medium: 209 <x < 272 g/d, n = 104; high: ≥272 g/d, n = 101)	Birth weight	Pen before weaning nested in batch[a]
	Weight gain from day − 7 to weaning day (low: ≤220 g/d, n = 101; medium: 220 <x < 300 g/d, n = 103; high: ≥300 g/d, n = 100)	Weight day − 7	
	Proportion of visits to feeder on day − 1 (low: 0% scans, n = 113; medium: 0 <x < 0.67% scans, n = 76; high: ≥0.66% scans, n = 104)		
	Proportion of visits to drinker on day − 1 (low: ≤0.22% scans, n = 50; medium: 0.22 <x < 0.66% scans, n = 110; high: ≥0.66% scans, n = 81)		
1	Weight gain from weaning day to day 1 (low: ≤−150 g/d, n = 86; medium: −150 <x < −75 g/d, n = 113; high: ≥−75 g/d, n = 104)	Weaning weight	Pen after weaning nested in batch[a]
	Proportion of visits to feeder on day 1 (low: ≤1.78% scans, n = 98; medium: 1.78 <x < 5.10% scans, n = 97; high: ≥5.10% scans, n = 97)		
	Proportion of visits to drinker on day 1 (low: ≤0.44% scans, n = 85; medium: 0.44 <x < 0.89% scans, n = 140; high: ≥0.89% scans, n = 67)		
2	Weight gain from weaning day to day 2 (low: ≤−67 g/d, n = 99; medium: −67 <x < 5 g/d, n = 103; high: ≥5 g/d, n = 100)		
	Weight gain from days 1–2 (low: ≤0 g/d, n = 109; medium: 0 <x < 167 g/d, n = 93; high: ≥167 g/d, n = 100)		
	Proportion of visits to feeder on day 1 (low: ≤1.78% scans, n = 97; medium: 1.78 <x < 5.11% scans, n = 97; high: ≥5.11% scans, n = 97)		
	Proportion of visits to drinker on day 1 (low: ≤0.44% scans, n = 85; medium: 0.44 <x < 0.89% scans, n = 140; high: ≥0.89% scans, n = 66)		

[a] Random effects accounted for differences within and between litters

normality and homoscedasticity and the effects of the measures of nutritional status was analysed with linear mixed-effects models with a Gaussian distribution. Due to high frequency of zeros, LOC on days 1 (49% zero observations) and 2 (26% zero observations), and SOC on days − 1 (67% zero observations), 1 (95% zero observations) and 2 (92% zero observations) were transformed into a binary variable (yes; no) and the effects of the measures of nutritional status were analysed with mixed-effects logistic regression models. The fit of the models was confirmed through graphical inspection of the residuals. Tukey-adjusted post-hoc analyses were performed for each model (library *emmeans* v.1.6.3; Lenth, 2021), except for the models assessing the effects of weight gain after weaning. For these models, Holm-adjusted post-hoc analyses were performed to control for multiplicity. Compact letters displaying pairwise comparisons were extracted from the post-hoc analyses using library multcomp v.14–20 (Hothorn et al., 2008).

The effects of the latencies to visit the feeder and drinker on day 1 and LOC and SOC on days 1 and 2 were analysed with Cox's proportional hazards mixed-effects model (libraries *survival* v.3.2–3, Therneau, 2020a; *coxme* v.2.2–16, Therneau, 2020b). Each model included play behaviour as binary variable (yes; no) as fixed effect, weaning weight as covariate, and pen after weaning nested in batch as random effect. The fit of the models was confirmed by assessing significance of the integrated log-link test.

2.5. Data availability

The raw dataset is available on Mendeley Data (Franchi et al., 2022a).

3. Results

The effects of weight gain, visits to feeder, visits to drinker, latency to visit the feeder and latency to visit the drinker on LOC and SOC are presented separately below. The effects of the "weight" covariates in their respective models (Table 2) were not statistically significant ($P > 0.1$).

3.1. *Weight gain and play*

Pigs in the low weight gain category from birth to weaning spent the shortest time performing LOC on day − 1 ($\chi^2_2 = 15.81$; $P < 0.001$; Fig. 2 A). Pigs in the low weight gain category from day − 7 to weaning spent the shortest time performing LOC on day − 1 ($\chi^2_2 = 10.58$; $P = 0.005$; Fig. 2B). No effect of weight gain from weaning to day 1 on LOC on day 1 was detected ($\chi^2_2 = 2.35$; $P = 0.308$; Fig. 2C). Pigs in the high (Odds Ratio (OR) = 3.9, 95% Confidence Interval (CI) [1.5–9.8]) and medium (OR = 2.8, 95% CI [1.2–6.4]) weight gain categories from weaning to day 2 showed higher odds of performing LOC on day 2 than pigs in the low weight gain category ($\chi^2_2 = 11.79$; $P = 0.003$; Fig. 2D). Pigs in the high weight gain category from days 1–2 showed higher odds of performing LOC on day 2 than pigs in the low weight gain category (OR = 2.9, 95% CI [1.2–7.1]; $\chi^2_2 = 6.46$; $P = 0.039$; Fig. 2E).

Pigs in the low weight gain category from birth to weaning showed the lowest odds of performing SOC on day − 1 ($OR_{L/M} = 0.2$, 95% CI [0.1–0.6]; $OR_{L/H} = 0.3$, 95% CI [0.1–0.7]; $\chi^2_2 = 12.79$; $P = 0.002$; Fig. 3A). Pigs in the low weight gain category from day − 7 to weaning showed the lowest odds of performing SOC on day − 1 than pigs in the low weight gain category ($OR_{L/M} = 0.4$, 95% CI [0.2–0.8]; $OR_{L/H} = 0.4$, 95% CI [0.1–1.0]; $\chi^2_2 = 6.47$; $P = 0.039$; Fig. 3B). Pigs in the high weight gain category from weaning to day 1 showed higher odds of performing SOC on day 1 than pigs in the medium weight gain category (OR = 16.9, 95% CI [1.5–192]; $\chi^2_2 = 8.64$; $P = 0.013$; Fig. 3C). No effect of weight gain from weaning to day 2 on SOC on day 2 was detected ($\chi^2_2 = 3.63$; $P = 0.163$; Fig. 3D). Pigs in the high weight gain category from days 1–2 tended to show the highest odds of performing SOC on day 2 ($OR_{H/L} = 3.1$, 95% CI [0.5–19.5]; $OR_{H/M} = 5.4$, 95% CI [1.0–28.7]; $\chi^2_2 = 4.99$; $P = 0.082$; Fig. 3E).

3.2. *Eating behaviour and play*

Pigs with medium proportion of visits to the feeder on day − 1 tended to spend the longest time performing LOC on day − 1 ($\chi^2_2 = 5.16$; $P = 0.075$; Fig. 4A). Pigs with low proportion of visits to the feeder on day 1 showed the lowest odds of performing LOC on day 1 ($OR_{L/M} = 0.3$, 95% CI [0.1–0.7]; $OR_{L/H} = 0.2$, 95% CI [0.1–0.7]; $\chi^2_2 = 8.62$; $P = 0.013$; Fig. 4B) and on day 2 ($OR_{L/M} = 0.2$, 95% CI [0.1–0.6]; $OR_{L/H} = 0.1$, 95% CI [0.03–0.3]; $\chi^2_2 = 17.07$; $P < 0.001$; Fig. 4C). Pigs performing LOC on day 1 did not differ from pigs not performing LOC on day 1 regarding latency to visit the feeder within the first 24 h from weaning ($\chi^2_1 = 0.24$; $P = 0.618$). Performance of LOC on day 2 was associated with a tendency for a sooner visit to the feeder within 24 h following weaning (Hazard Rate Ratio (HRR) = 1.3, 95% CI [1.0–1.7]; $\chi^2_1 = 3.62$; $P = 0.057$).

No effect of proportion of visits to the feeder on SOC was detected on any of the investigated days (SOC_{day-1} vs. $Visits_{day-1}$: $\chi^2_2 = 0.60$, $P = 0.739$; SOC_{day1} vs. $Visits_{day1}$: $\chi^2_2 = 2.03$, $P = 0.363$; SOC_{day2} vs. $Visits_{day1}$: $\chi^2_2 = 4.10$, $P = 0.128$). Pigs not performing SOC did not differ from pigs performing SOC on day 1 ($\chi^2_1 = 1.02$; $P = 0.313$) and day 2 ($\chi^2_1 = 1.14$; $P = 0.287$) in latency to visit the feeder within 24 h from weaning.

3.3. *Drinking behaviour and play*

Pigs with low proportion of visits to the drinker on day − 1 spent the shortest time performing LOC on day − 1 ($\chi^2_2 = 13.26$; $P = 0.001$; Fig. 5A). No effect of proportion of visits to the drinker on day 1 on LOC on day 1 was detected ($\chi^2_2 = 1.42$; $P = 0.492$; Fig. 5B). Pigs with low proportion of visits to the drinker on day 1 showed higher odds of performing LOC on day 2 than pigs with medium proportion of visits to the drinker on day 1 (OR = 3.2, 95% CI [1.4–7.1]; $\chi^2_2 = 8.83$; $P = 0.012$; Fig. 5C). Pigs not performing LOC did not differ from pigs performing LOC on day 1 in latency to visit the drinker within 24 h from weaning ($\chi^2_1 = 0.75$; $P = 0.387$). Performance of LOC on day 2 was associated with a sooner visit to the feeder within 24 h following weaning (Hazard Rate Ratio (HRR) = 1.4, 95% CI [1.1–1.7]; $\chi^2_1 = 4.06$; $P = 0.044$).

No effect of proportion of visits to the drinker on SOC was detected on any of the investigated days (SOC_{day-1} vs. $Visits_{day-1}$: $\chi^2_2 = 4.16$, $P = 0.125$; SOC_{day1} vs. $Visits_{day1}$: $\chi^2_2 = 1.48$, $P = 0.477$; SOC_{day2} vs. $Visits_{day1}$: $\chi^2_2 = 0.31$, $P = 0.859$). Pigs not performing SOC did not differ from pigs performing SOC on day 1 ($\chi^2_1 = 0.01$; $P = 0.928$) and day 2 ($\chi^2_1 = 0.89$; $P = 0.344$) in latency to visit the drinker within 24 h from weaning.

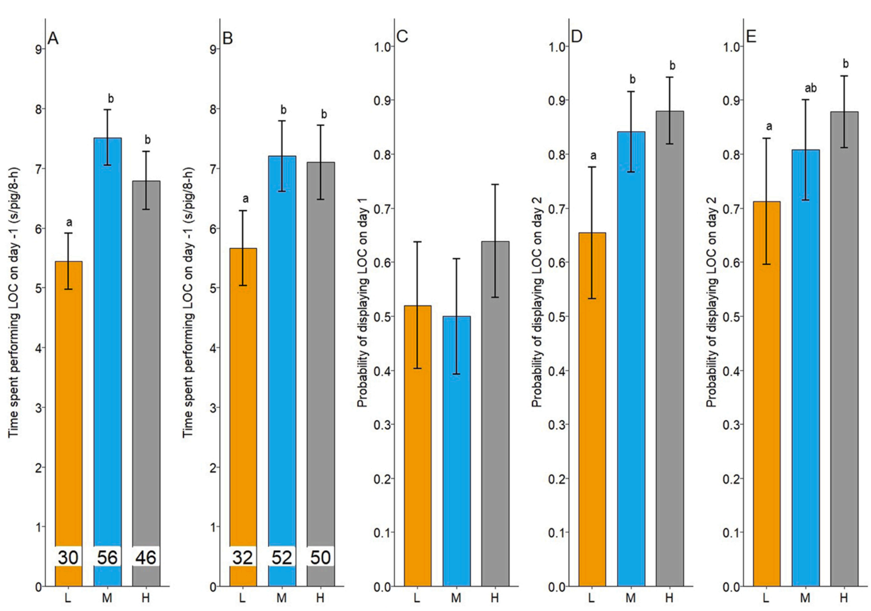

Fig. 2. Relationship between weight gain (A: from birth to weaning; B: from day −7 to weaning; C: from weaning to day 1; D: from weaning to day 2; E: from days 1–2) and locomotor-rotational play (LOC) registered on days − 1 (A and B), 1 (C) and 2 (D and E) relative to weaning between 14:00 h and 22:00 h. The weight gain categories were low (L; orange bars), medium (M; blue bars), and high (H; grey bars). In sub-Figs. A and B, bars indicate least squares means of durations of LOC (s/pig/8-h) and error bars indicate standard error, square-root-transformed prior to analysis. The back-transformed least squares means are shown inside white boxes within each bar. In sub-figures C, D and E, bars indicate probability of displaying LOC and error bars indicate standard error, both back-transformed from the model using the inverse link function. Different superscript letters indicate statistical difference at $P < 0.05$ within days.

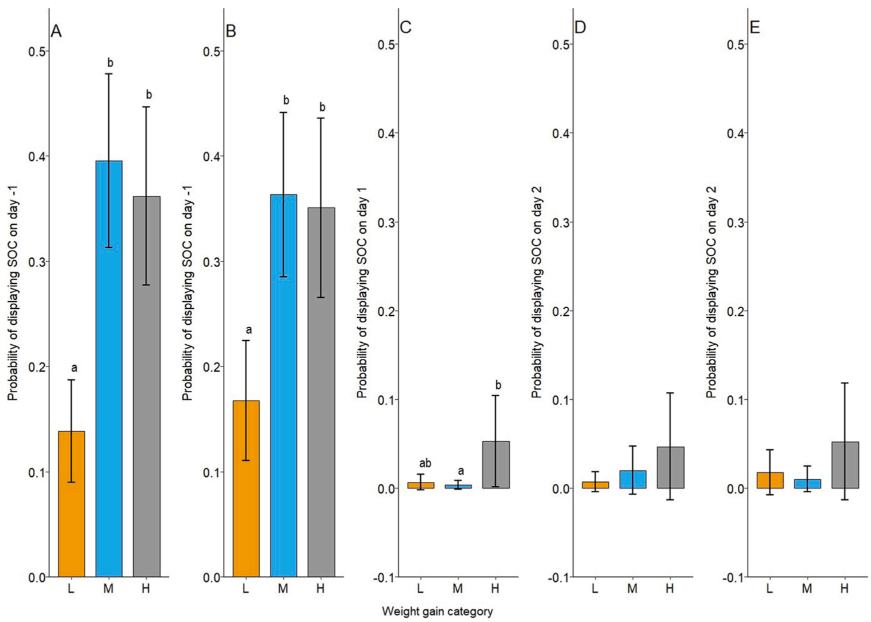

Fig. 3. Relationship between weight gain (A: from birth to weaning; B: from day −7 to weaning; C: from weaning to day 1; D: from weaning to day 2; E: from days 1–2) and probability of displaying social play (SOC) on each day relative to weaning (days −1 (A and B), 1 (C) and 2 (D and E)) between 14:00 h and 22:00 h. The weight gain categories were low (L; orange bars), medium (M; blue bars), and high (H; grey bars). The bars represent probability, and the error bars indicate standard error. Estimates and standard error bars were back-transformed from the model using the inverse link function. Different superscript letters indicate statistical difference at $P < 0.05$ within days.

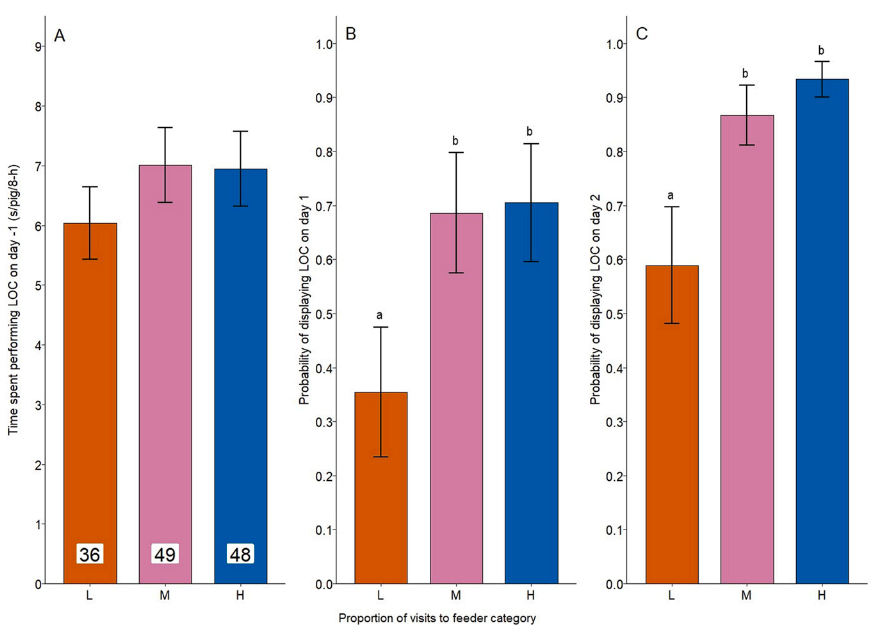

Fig. 4. Relationship between proportion of visits to the feeder (A: day −1; B and C: both day 1) and locomotor-rotational play (LOC) registered on days − 1 (A), 1 (B) and 2 (C) relative to weaning between 14:00 h and 22:00 h. The proportion of visits to feeder categories were low (L; red bars), medium (M; pink bars), and high (H; dark blue bars). In sub-figure A, bars indicate least squares means of durations of LOC (s/pig/8-h) and error bars indicate standard error, square-root-transformed prior to analysis. The back-transformed least squares means are shown inside white boxes within each bar. In sub-Figs. B and C, bars indicate probability of displaying LOC and error bars indicate standard error, both back-transformed from the model using the inverse link function. Different superscript letters indicate statistical difference at $P < 0.05$ within days.

4. Discussion

4.1. Play behaviour and weight gain

We found that weight gain, which is indicative of well-nourished individuals, positively related to LOC before and after weaning, except in the first 24 h post weaning. In the current study, the weight gain from birth to weaning reflected pigs' development (long-term) and the weight gain from day − 7 to weaning reflected pigs' nutritional status pre-weaning (short-term). Our results agree with previous studies examining play behaviour in weaner pigs. For instance, Brown et al. (2015) found a positive relationship between weight gain and LOC pre-weaning. Moreover, Šilerová et al. (2010) found that LOC on day 5 post-weaning and weight gain during the 5 days following weaning were positively related. Within the first 24 h following weaning, all three weight gain categories displayed weight loss (Table 2) and all pigs showed a dramatic decline in time spent playing (Franchi et al., 2022b), illustrating the negative effects of early, abrupt weaning (i.e., separation from the sow, environmental change, and social stress). This may explain the absence of a clear relationship between LOC and weight gain during this day. Given that animals are motivated to play when their basic needs, such as food, are met (Boissy et al., 2007; Held and Špinka, 2011), the lower motivation to perform LOC by the pigs losing weight following weaning was likely due to undernourishment and a motivational shift toward feeding and conserving body energy reserves (Burghardt, 1984; Jensen et al., 2015). Even though play behaviour typically comprises a small proportion of an animal's activity time budget (Martin and Caro, 1985), the performance of this behaviour, known to involve a high degree of energy expenditure (Müller-Schwarze et al., 1982), may be sacrificed when body energy reserves or food supply are low (Sommer and Mendoza-Granados, 1995; Nunes et al., 2004). Additionally, we cannot exclude that the pigs' motivation may also have shifted toward

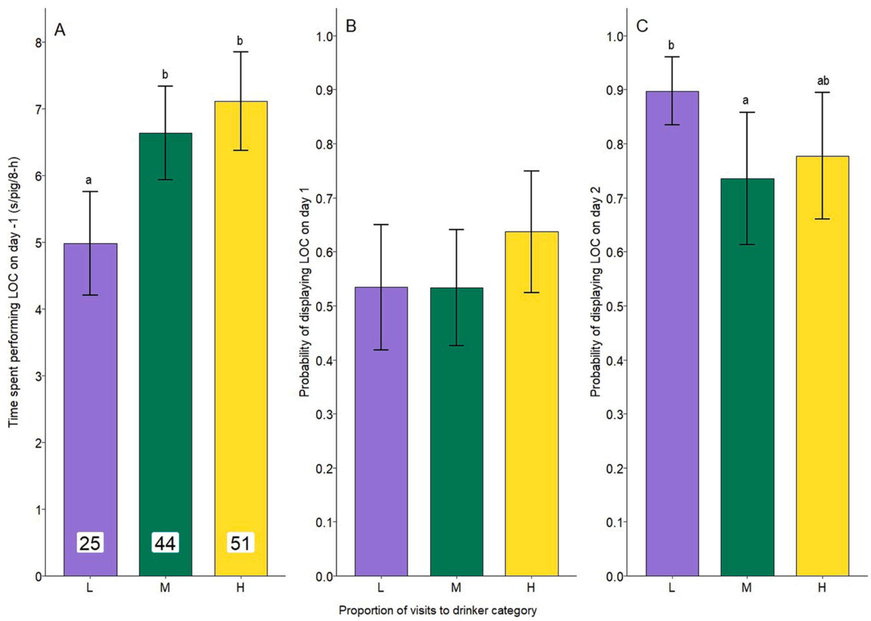

Fig. 5. Relationship between proportion of visits to the drinker (A: day −1; B and C: both day 1) and locomotor-rotational play (LOC) registered on days − 1 (A), 1 (B) and 2 (C) relative to weaning between 14:00 h and 22:00 h. The proportion of visits to drinker categories were low (L; purple bars), medium (M; green bars), and high (H; yellow bars). In sub-figure A, bars indicate least squares means of durations of LOC (s/pig/8-h) and error bars indicate standard error, square-root-transformed prior to analysis. The back-transformed least squares means are shown inside white boxes within each bar. In sub-Figs. B and C, bars indicate probability of displaying LOC and error bars indicate standard error, both back-transformed from the model using the inverse link function. Different superscript letters indicate statistical difference at $P < 0.05$ within days.

exploring the novel environment and defending social status during the establishment of a novel hierarchy (D'Eath, 2005; Weary et al., 2008).

The relationship between SOC and weight gain was the clearest in the pre-weaning period: pigs in the high and medium weight gain categories had higher odds of performing SOC than pigs in the low weight gain category. Similar findings were reported by Brown et al. (2015) in pigs during the pre-weaning period and by Nunes et al., (1999, 2004) in ground squirrels (*Spermophilus beldingi*). Like LOC, SOC involves a considerable degree of energy expenditure in addition to requiring a socially stable environment, which was likely achieved throughout the weeks pre-weaning, but disrupted in the first days following weaning, and especially, in the pigs that were moved and socially mixed in a novel environment (Newberry et al., 1988; Brown et al., 2015). Therefore, the positive relationship between SOC and weight gain pre-weaning was expected. Conversely, no clear relationship between SOC and weight gain post-weaning was observed. Likewise, Brown et al. (2018) reported no relationship between SOC and weight gain in pigs after weaning. As demonstrated by Franchi et al., (2022b), accounting for the current study's population, the performance of both LOC and SOC decreased considerably during the first 48 h following weaning compared to the pre-weaning levels. Additionally, SOC was defined herein as two or more pigs mutually engaging in, at least, one of the behaviours constituting SOC, while in other studies this mutuality was not a prerequisite (e.g., Hötzel et al., 2010; Camerlink et al., 2021). Hence, the combination of the negative effect of abrupt and early weaning (e.g., regrouping, novel environment; Donaldson et al., 2002) and a stricter SOC definition, resulting in a low level of SOC, may explain why the present study found no clear relationship between SOC and weight gain post-weaning. As it is unclear whether LOC and SOC share similar motivation and whether they are similarly affected by contextual changes, we advise future studies to investigate the motivations for each type of play and how this is influenced by nutritional, as well as social and health, status.

4.2. Play behaviour and feeding and drinking behaviour

To our knowledge, this is the first study examining the relationship between play behaviour and measures of feeding behaviour in pigs. In the current study, no clear relationship between play behaviour and visits to the feeder was observed before weaning. We speculate that this finding is due to pigs being able to fulfil their nutritional requirements by suckling the sow, resulting in a low frequency of visits to the feeder (Table 2). The solid feed available pre-weaning was sow lactation diet, which was not intended to be a primary source of feed for the piglets but rather the possibility of visiting the sow feeder should be seen as a social learning facilitator, so that pigs could learn to ingest solid feed from their mother (Oostindjer et al., 2011) to facilitate solid feed intake post weaning. Before weaning, pigs displaying a low frequency of visits to the drinker spent the shortest time performing LOC. Water intake is an intrinsic aspect of the nutrition, health, and welfare of pigs (Andersen et al., 2014), and variations in water intake can indicate ill health (Pijpers et al., 1991) or thermal stress (Pearce et al., 2014). As play behaviour involves energy and nutrient expenditure (Müller-Schwarze et al., 1982), a higher drinking frequency, and potentially higher water intake, could have been a way to restore water and nutrients expended during play (Bigelow and Houpt, 1988).

We found that pigs showing medium and high frequency of visits to the feeder on day 1 showed higher odds of displaying LOC on the two days after weaning than pigs showing low frequency of visits to the feeder on day 1. Additionally, the performance of LOC on day 2 was associated with a shorter latency to visit to the feeder and the drinker on the previous day. These results suggest that those pigs that were able to compensate the loss of milk at weaning by visiting these resources sooner and increasing their intake of solid feed and water were better nourished and thus more motivated to play, supporting the findings on the relation between weight gain and LOC. Winters et al. (2022) also demonstrated that pigs showing shorter latency to visit these resources were the ones with higher pre-weaning weight gain and higher visits to the feeder on day − 1.

In our study, all pigs were subjected to some degree of novelty after weaning. Pigs kept in the farrowing pen dealt with the weaning from the sow and introduction of a novel feed. Pigs moved to a weaner pen additionally experienced a new environment (including new feeder and drinker) and new peers. As discussed above, the motivations for each type of play behaviour likely vary beyond the individual nutritional status. This may further explain the lack of clear relationships between feeding and drinking behaviour and SOC. Irrespective, in the present study, the outcomes of the analyses of the effects of the nutritional measures on the two types of play behaviour must be interpreted cautiously, due to the low daily proportions of visits to each resource registered in each category (Table 2) as well as the low levels of each type of play behaviour, particularly after weaning. We encourage more studies to assess the influence of other aspects than nutrition, such as presence of illness, on the variation in LOC and SOC in pigs around weaning.

4.3. Value of play as a positive animal welfare measure

In our study, the performance of play behaviour was positively related to the display of clinical and behavioural signs of being well-nourished. This association with the lack of a welfare threat (e.g., undernourishment or hunger) and a putative positive experience (e.g., satiation) means that increased play behaviour may be an indicator of increased welfare and as such as a positive welfare indicator (Held and Špinka, 2011). However, we acknowledge that this covers a range of the welfare spectrum, and in our study, play behaviour cannot be interpreted as an indicator of *absolute* positive affective state because we are not able to distinguish between the pigs who were merely coping with weaning from the pigs who were truly thriving, if we can speak of thriving during an abrupt, early weaning (Ahloy-Dallaire et al., 2018; Maple and Bloomsmith, 2018). To enable the experience of true positive affective states in animals, appropriate nutrition, as well as social and physical environment, are required (Franchi et al., 2022b; Maple and Bloomsmith, 2018). This study shows that animals experiencing a more stable condition (i.e., by being better nourished) are motivated to perform more play behaviour. For play behaviour to indicate the presence of positive affective states, it should increase when positive conditions become even more positive (Ahloy-Dallaire et al., 2018), and this should also be demonstrated in other (more) positive contexts than weaning. Hence, we advise continuation of the validation of play against physiological (e.g., stress hormones, peripheral body temperature), clinical (e.g., presence of disease or injuries), behavioural (e.g., body postures), and cognitive measures (e.g., cognitive bias, reward loss sensitivity) (as reviewed by Kremer et al., 2020) to understand and confirm the value of play behaviour as a positive animal welfare indicator.

5. Conclusions

Our results support the hypothesis that animals experiencing a more stable condition (e.g., better nourishment) are more motivated to perform play behaviour. The current study represents an advancement in the understanding and validation of play behaviour as an animal welfare indicator.

CRediT authorship contribution statement

Guilherme A. Franchi: Conceptualization, Investigation, Methodology, Data curation, Visualization, Formal analysis, Software. **Mona L. V. Larsen:** Conceptualization, Investigation, Methodology, Funding acquisition, Resources, Project administration, Supervision. **Ida H. Kristoffersen:** Data curation, Visualization. **Jeanet F.M. Winters:** Conceptualization, Investigation, Methodology. **Lene Juul Pedersen:** Conceptualization, Investigation, Methodology, Funding acquisition, Resources, Project administration, Supervision. **Margit Bak Jensen:** Conceptualization, Investigation, Methodology, Funding acquisition, Resources. All authors contributed to the article and approved the submitted version.

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.

Acknowledgments

The authors acknowledge the help from the staff at the Pig Research Unit, Aarhus University (AU-Viborg), Denmark. We also thank Carsten Kjærulff Christensen and Dines Thøger Bolt (both AU) for assistance with pig handling and behavioural observations. This manuscript is developed as part of a project funded by the European Union's Horizon 2020 research and innovation programme under grant agreement No. 862919. The data collection as well as the writing of this manuscript was further funded by the Ministry of Food, Agriculture and Fisheries of Denmark under the program "Veterinary agreement III" (Veterinærforlig III, AU6), and by the Marie Skłodowska-Curie Action grant agreement No. 842555 (project AutoPlayPig).

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.

Andersen, H.L., Dybkjær, L., Herskin, M.S., 2014. Growing pigs' drinking behaviour: number of visits, duration, water intake and diurnal variation. Animal 8, 1881–1888. https://doi.org/10.1017/S175173111400192X.

Bateson, M., Martin, P., 2021. Measuring Behaviour: An Introductory Guide, fourth ed. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/9781108776462.

Bateson, P., Mendl, M., Feaver, J., 1990. Play in the domestic cat is enhanced by rationing of the mother during lactation. Anim. Behav. 40, 514–525. https://doi.org/10.1016/S0003-3472(05)80532-9.

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.

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., 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.

Brooks, M.E., Kristensen, K., van Benthem, K.J., 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, S.M., Klaffenböck, M., Nevison, I.M., Lawrence, A.B., 2015. Evidence for litter differences in play behaviour in pre-weaned pigs. Appl. Anim. Behav. Sci. 172, 17–25. https://doi.org/10.1016/j.applanim.2015.09.007.

Brown, S.M., Peters, R., Nevison, I.M., Lawrence, A.B., 2018. Playful pigs: evidence of consistency and change in play depending on litter and developmental stage. Appl. Anim. Behav. Sci. 198, 36–43. https://doi.org/10.1016/j.applanim.2017.09.018.

Burgdorf, J., Panksepp, J., 2007. The neurobiology of positive emotions. Neurosci. Biobehav. Rev. 30, 173–187. https://doi.org/10.1016/j.neubiorev.2005.06.001.

Burghardt, G.M., 1984. On the origins of play. In: Smith, P.K. (Ed.), Play in Animals and Humans. Blackwell, Oxford, pp. 5–41.

Burghardt, G.M., 2005. The Genesis of Animal Play: Testing the Limits. MIT Press.

Camerlink, I., Proßegger, C., Kubala, D., Galunder, K., Rault, J.L., 2021. Keeping littermates together instead of social mixing benefits pig social behaviour and growth post-weaning. Appl. Anim. Behav. Sci. 235, 105230 https://doi.org/10.1016/j.applanim.2021.105230.

D'Eath, R.B., 2005. Socialising piglets before weaning improves social hierarchy formation when pigs are mixed postweaning. Appl. Anim. Behav. Sci. 93, 199–211. https://doi.org/10.1016/j.applanim.2004.11.019.

Donaldson, T.M., Newberry, R.C., Špinka, M., Cloutier, S., 2002. Effects of early play experience on play behaviour of piglets after weaning. Appl. Anim. Behav. Sci. 79, 221–231. https://doi.org/10.1016/S0168-1591(02)00138-7.

Du Sert, N.P., Ahluwalia, A., Alam, S., Avey, M.T., Baker, M., Browne, W.J., Clark, A., Cuthill, I.C., Dirnagl, U., Emerson, M., Garner, P., 2020. Reporting animal research: explanation and elaboration for the ARRIVE guidelines 2.0. PLoS Biol. 18, e3000411 https://doi.org/10.1371/journal.pbio.3000411.

Duve, L.R., Weary, D.M., Halekoh, U., Jensen, M.B., 2012. The effects of social contact and milk allowance on responses to handling, play, and social behavior in young dairy calves. J. Dairy Sci. 95, 6571–6581. https://doi.org/10.3168/jds.2011-5170.

Franchi, G.A., Larsen, M.L.V., Kristoffersen, I.H., Winters, J.F.M., Jensen, M.B., Pedersen, L.J., 2022a. Supplemental material: play behaviour positively relates with growth, feeding behaviour and drinking behaviour in weaner pigs (*Sus scrofa*). Mendeley Data v1. 10.17632/n6hsg8kcjf.1.

Franchi, G.A., Larsen, M.L.V., Winters, J.F.M., Jensen, M.B., Pedersen, L.J., 2022b. Investigating the effects of two weaning methods and two genetic hybrids on play behaviour in weaner pigs (*Sus scrofa*). Front. Anim. Sci. 3, 909038 https://doi.org/10.3389/fanim.2022.909038.

Hall, S.L., Bradshaw, J.W., 1998. The influence of hunger on object play by adult domestic cats. Appl. Anim. Behav. Sci. 58, 143–150. https://doi.org/10.1016/S0168-1591(97)00136-6.

Held, S.D., Špinka, M., 2011. Animal play and animal welfare. Anim. Behav. 81, 891–899. https://doi.org/10.1016/j.anbehav.2011.01.007.

Hinkle, D.E., Wiersma, W., Jurs, S.G., 2003. Applied Statistics for the Behavioural Sciences, hird ed. Houghton Mifflin,, Boston, MA, USA.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.

Hötzel, M.J., Machado Filho, L.C.P., Irgang, R., Alexandre Filho, L., 2010. Short-term behavioural effects of weaning age in outdoor-reared piglets. Animal 4, 102–107. https://doi.org/10.1017/S1751731109990875.

Jensen, M.B., Duve, L.R., Weary, D.M., 2015. Pair housing and enhanced milk allowance increase play behavior and improve performance in dairy calves. J. Dairy Sci. 98, 2568–2575. https://doi.org/10.3168/jds.2014-8272.
Jensen, P., Stangel, G., 1992. Behaviour of piglets during weaning in a seminatural enclosure. Appl. Anim. Behav. Sci. 33, 227–238. https://doi.org/10.1016/S0168-1591(05)80010-3.
Lawrence, I., Lin, K., 1989. A concordance correlation coefficient to evaluate reproducibility. Biometrics 255–268. https://doi.org/10.2307/2532051.
Lenth, R.V. (2021). emmeans: estimated marginal means, aka least-squares means. R package version 1.6.3. ⟨https://CRAN.R-project.org/package=emmeans⟩ (accessed 01 June 2022).
Loranca, A., Torrero, C., Salas, M., 1999. Development of play behavior in neonatally undernourished rats. Physiol. Behav. 66, 3–10. https://doi.org/10.1016/S0031-9384(98)00235-2.
Loy, J., 1970. Behavioral responses of free-ranging rhesus monkeys to food shortage. Am. J. Phys. Anthropol. 33, 263–271. https://doi.org/10.1002/ajpa.1330330212.
Maple, T.L., Bloomsmith, M.A., 2018. Introduction: the science and practice of optimal animal welfare. Behav. Process. 156, 1–2. https://doi.org/10.1016/j.beproc.2017.09.012.
Martin, P., Caro, T.M., 1985. On the functions of play and its role in behavioral development. In: Advances in the Study of Behavior, Vol. 15. Academic Press, pp. 59–103. https://doi.org/10.1016/S0065-3454(08)60487-8.
Miguel-Pacheco, G.G., Vaughan, A., de Passillé, A.M., Rushen, J., 2015. Relationship between locomotor play of dairy calves and their weight gains and energy intakes around weaning. Animal 9, 1038–1044. https://doi.org/10.1017/S1751731115000063.
Müller-Schwarze, D., Stagge, B., Muller-Schwarze, C., 1982. Play behavior: persistence, decrease, and energetic compensation during food shortage in deer fawns. Science 215, 85–87 science.215.4528.85.
Newberry, R.C., Wood-Gush, D.G.M., Hall, J.W., 1988. Playful behaviour of piglets. Behav. Process. 17, 205–216. https://doi.org/10.1016/0376-6357(88)90004-6.
Nunes, S., Muecke, E.M., Anthony, J.A., Batterbee, A.S., 1999. Endocrine and energetic mediation of play behavior in free-living Belding's ground squirrels. Horm. Behav. 36, 153–165. https://doi.org/10.1006/hbeh.1999.1538.
Nunes, S., Muecke, E.M., Lancaster, L.T., Miller, N.A., Mueller, M.A., Muelhaus, J., Castro, L., 2004. Functions and consequences of play behaviour in juvenile Belding's ground squirrels. Anim. Behav. 68, 27–37. https://doi.org/10.1016/j.anbehav.2003.06.024.
Oostindjer, M., Bolhuis, J.E., Mendl, M., Held, S., van den Brand, H., Kemp, B., 2011. Learning how to eat like a pig: effectiveness of mechanisms for vertical social learning in piglets. Anim. Behav. 82, 503–511. https://doi.org/10.1016/j.anbehav.2011.05.031.
Pearce, S.C., Sanz-Fernandez, M.V., Hollis, J.H., Baumgard, L.H., Gabler, N.K., 2014. Short-term exposure to heat stress attenuates appetite and intestinal integrity in growing pigs. J. Anim. Sci. 92, 5444–5454. https://doi.org/10.2527/jas.2014-8407.
Pijpers, A., Schoevers, E.J., Van Gogh, H., van Leengoed, L.A.M.G., Visser, I.J.R., van Miert, A.S.J.P.A.M., Verheijden, J.H.M., 1991. The influence of disease on feed and water consumption and on pharmacokinetics of orally administered oxytetracycline in pigs. J. Anim. Sci. 69, 2947–2954. https://doi.org/10.2527/1991.6972947x.
R Core Team. (2021). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available online at: ⟨https://www.R-project.org/⟩ (accessed 01 June 2022).
Rushen, J., Wright, R., Johnsen, J.F., Mejdell, C.M., de Passillé, A.M., 2016. Reduced locomotor play behaviour of dairy calves following separation from the mother reflects their response to reduced energy intake. Appl. Anim. Behav. Sci. 177, 6–11. https://doi.org/10.1016/j.applanim.2016.01.023.
Sharpe, L.L., Clutton-Brock, T.H., Brotherton, P.N., Cameron, E.Z., Cherry, M.I., 2002. Experimental provisioning increases play in free-ranging meerkats. Anim. Behav. 64, 113–121. https://doi.org/10.1006/anbe.2002.3031.
Šilerová, J., Špinka, M., Šárová, R., Algers, B., 2010. Playing and fighting by piglets around weaning on farms, employing individual or group housing of lactating sows. Appl. Anim. Behav. Sci. 124, 83–89. https://doi.org/10.1016/j.applanim.2010.02.003.
Siviy, S.M., Bekoff, M., Beyers, J.A., 1998. Neurobiological substrates of play behavior. Animal play. Evolutionary, Comparative and Ecological Perspectives. Cambridge University Press, Cambridge, UK, pp. 221–242.
Sommer, V., Mendoza-Granados, D., 1995. Play as indicator of habitat quality: a field study of langur monkeys (Presbytis entellus. Ethology 99, 177–192. https://doi.org/10.1111/j.1439-0310.1995.tb00893.x.
Špinka, M., 2017. In: Jensen, P. (Ed.), "Behaviour of Pigs" in the Ethology of Domestic Animals, third ed. CAB International Publishing, pp. 214–227.
Špinka, M., Newberry, R.C., Bekoff, M., 2001. Mammalian play: training for the unexpected. Q. Rev. Biol. 76, 141–168. https://doi.org/10.1086/393866.
Therneau, T. (2020a). A package for survival analysis in R. R package version 3.2–3. ⟨https://CRAN.R-project.org/package=survival⟩ (accessed 01 June 2022).
Therneau, T.M. (2020b). coxme: mixed effects Cox models. R package version 2.2–16. ⟨https://CRAN.R-project.org/package=coxme⟩ (accessed 01 June 2022).
Weary, D.M., Jasper, J., Hötzel, M.J., 2008. Understanding weaning distress. Appl. Anim. Behav. Sci. 110, 24–41. https://doi.org/10.1016/j.applanim.2007.03.025.
Winters, J.F.M., Foldager, L., Pedersen, L.J., 2022. Postweaning growth and feeding behaviour in pigs: effect of heavier hybrid and weaning intact litters in farrowing pens for loose-housed sows. Animal, 100688. https://doi.org/10.1016/j.animal.2022.100688.
Yeates, J.W., Main, D.C., 2008. Assessment of positive welfare: a review. Vet. J. 175, 293–300. https://doi.org/10.1016/j.tvjl.2007.05.009.