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ABSTRACT

Nowadays, most pigs are raised indoors, on intensive farms providing a poor environment. In these conditions, the risk of the occurrence of damaging behaviours is high, with dramatic consequences for animal health and welfare as well as economic losses for farmers. Early-life conditions may predispose individuals to develop damaging behaviours later in life. In contrast, reinforcing affiliative behaviours between piglets before weaning might help to prevent tail-biting episodes. In this field study, we aimed at improving early-life conditions of piglets on a commercial farm by completely suppressing painful procedures and staggering their exposure to weaning stress factors. The alternative early-life management strategy combined housing in free-farrowing pens with temporary crating of the sow, socialisation during the lactation period with whole-life maintenance of the hierarchical groups, and delayed transfer to the post-weaning room after sow removal. Control conditions included birth in farrowing crates, tail docking, absence of socialisation during the lactation period, abrupt weaning with immediate transfer to the post-weaning room and mixing with non-littermates. We evaluated the health, welfare, and performance of alternatively raised pigs (n = 80) as compared to controls (n = 75). Visits were made throughout the lifespan of individuals to evaluate their growth and health status. Body and tail lesions were scored as proxy measures of aggressiveness and impaired welfare. Blood and bristle samples were periodically collected to evaluate stress, inflammation and immune competence. While the whole-life performance of pigs was similar among groups, the alternative early-life conditions prevented the growth slowdown usually observed after weaning. In addition, alternatively raised pigs displayed more neutrophils, eosinophils and monocytes the day after weaning, as well as higher C-Reactive Protein levels. One week later, their monocytes displayed greater phagocytic capacity. Altogether, these data suggest an enhanced innate immune competence for alternatively raised pigs around weaning. Piglets reared under alternative conditions also exhibited fewer and less severe body lesions than standard pigs, one week after weaning. In contrast, they showed more tail lesions on days 36 and 66 associated with greater levels of acute phase proteins (C-Reactive Protein and haptoglobin). To conclude, alternative early-life management better prepared piglets for weaning. However, the whole-life maintenance of early-established social groups was not sufficient to prevent the occurrence of damaging behaviours in undocked pigs.

Implications

The increasing consideration of European citizens for animal welfare stresses the need to implement on-farm strategies to improve farm animals' living conditions. The pig industry is particularly concerned, with more than 90% of pigs raised indoors, in intensive systems with poor early-life conditions, high stocking density, and lack of enrichment materials. We report herein how an improved early-life management, which includes the socialisation of suckling piglets, could better prepare them for weaning (increased innate immunity and decreased growth slowdown) while not affecting their whole-life performance. However, additional strategies are still needed to stop tail docking.

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Introduction

In mammals, the postnatal period is crucial for the complete maturation of the newborn, with long-term consequences for health and welfare. In particular, the early-life colonisation of mucosae by microorganisms shapes the immune competence of the individuals (reviewed by Henneke et al., 2021). Maternal care and peer interactions have further been shown to condition behaviour and brain function (reviewed by Branchi and Cirulli, 2014). Thus, optimised early-life conditions might constitute the foundations for good lifelong health.

In France, as in other European countries, most pigs are raised on intensive farms, providing a poor environment. Sows are commonly confined in farrowing crates during the whole lactation period, which negatively impacts not only their welfare but also maternal care and piglet development. The use of free-farrowing pens has been introduced to improve the life conditions of the sows and their offspring. Indeed, this kind of pen is usually larger and allows the sow to explore the environment freely and to raise its piglets through learning by example. This strategy has been shown to improve piglet performance and to limit the occurrence of damaging behaviours such as tail biting (Morgan et al., 2021; Kinane et al., 2021).

In intensive farming, during the first week of life, piglets generally undergo painful procedures such as tail docking, tooth clipping, and castration for males. For example, tail docking rapidly induces a rise in circulating cortisol levels and vocalisations as well as behavioural modifications in piglets until weaning (Numberger et al., 2016; Tallet et al., 2019). Although routine tail docking has been banned in the European Union, it is still widely used on farms to limit damaging behaviours. Indeed, the risk of tail injury is high in intensive farming and associated with animal pain and distress that concern both the biter and its victim. Because of its multifactorial nature, tail biting is difficult to control and it has dramatic consequences for animal health, welfare and performance associated with economic losses (Valros and Heinonen, 2015). In intensive farming, weaning, which occurs after only four weeks of life, is a particularly traumatic step, marked by concomitant maternal deprivation, diet change, vaccination, transfer to the postweaning room and mixing with non-littermates. All these challenges trigger stress responses characterised by increased cortisol levels (Colson et al., 2012).

In contrast, in natural conditions, weaning is progressive, beginning at four weeks of age and lasting more than two months (Jensen, 1986). Also, from the second week of life, piglets begin to leave the nest and to interact with non-littermates (Jensen and Redbo, 1987). At this period, positive interactions without intense agonistic behaviours take place. This early-life window of greater tolerance to unfamiliar conspecifics facilitates the integration of piglets into larger social groups and the subsequent development of their social and cognitive capacities. On pig farms, while social interactions between piglets are usually limited to littermates during the suckling period, it has also been observed that early-socialised piglets are prone to establish a hierarchy with unfamiliar congeners more quickly (D'Eath, 2005). Early socialisation of piglets has also been shown to increase play behaviours between piglets (Salazar et al., 2018) and to reduce aggressive behaviours the day after weaning (Camerlink et al., 2018).

In this context, we aim at improving the welfare of pigs raised on intensive farms without affecting their health and performance. For this purpose, we sought to upgrade early-life conditions of piglets by completely suppressing painful procedures and staggering their exposure to weaning stress factors. This alternative early-life management strategy combined housing in free-farrowing pens with temporary crating of the sow, socialisation during the lactation period, whole-life maintenance of the hierarchical group, and delayed transfer to the postweaning room after separation from the sow. In this article, we report the results of a clinical study conducted on a conventional farm. We describe the effects of our alternative early-life management strategy on the performance, health, and welfare of pigs from birth to slaughter, as compared to the standard one.

Material and methods

Ethical statement

The study was carried out in accordance with Directive 2010/63/EU and the Oniris ethics committee for veterinary clinical and epidemiological research approved the experimental protocol (CERVO-2020-22-V). Written informed consent was obtained from the owners for the inclusion of their animals in this study.

Animals, farm and experimental design

The experiment was performed on a breeder-fattener farm in the West of France (Ille-et-Vilaine). The farm housed 228 sows for an average production of 5 000 fattening pigs per year, "raised without antibiotics". It operated with a 5-week batch management system. In this study, we followed 12 litters issued from sows of comparable parity (P = 0.15), distributed over 3 batches in 2021. Detailed information about sow parity, litter size, and the mortality rate is given in Supplementary Table S1. A total of 155 commercial pigs (79 males and 76 females) of Nucleus genetics [Pietrain × (Landrace × Large White)] were included, each individually identified by radio frequency identification tags. In both groups, the piglets were not castrated, their teeth were not clipped and they were all vaccinated against type 2 Porcine Circovirus (**PCV2**) and *Mycoplasma hyopneumoniae* (Porcilis® PCV M Hyo, MSD, Beaucouzé, France) just before weaning at around 28 days of age. All piglets were fed the same diet adapted to their nutritional needs according to their age.

In each batch, two litters were included per treatment (Conventional and Alternative Early-Life Management, **C-ELM** and **A-ELM,** respectively) with similar enrichment (hessian sacks). In the conventional group, the two sows were housed in individual pens with farrowing crates and the piglets were not mixed before weaning. The pens measured 1.7 × 2.5 m comprising a heated nest of 0.6 m^2. Around day 28, piglets were moved to a postweaning pen and mixed. In the alternative group, two sows and their offspring were housed in adjacent farrowing pens, with the sows being restrained for only 2 days after farrowing. The pens measured 2.7 × 2.8 m including a 1.2 m^2 heated kennel. Piglets were socialised during the lactation period from 9 days of age *via* a tunnel connecting the two kennels (Supplementary Fig. S1). In the alternative condition, piglets were not tail docked and, at weaning, sows were removed while piglets were maintained in their familiar environment for three more days before transfer to the postweaning room. For both treatments, the transfer of the pigs to fattening pens was done without mixing.

Piglets from both treatments were housed in adjacent rooms during the postweaning period and in adjacent pens of the same room during fattening. The size of the postweaning and fattening pens was identical for both treatments (2 × 5.4 m and 4.5 × 5 m, respectively) with similar enrichment (hessian sacks and chains or hardwoods) and access to food and water. For each batch, all pigs (C- and A-ELM) were sent on the same day to the Cooperl slaughterhouse in Montfort-sur-Meu (Ille-et-Vilaine, France) at an average age of 155 ± 1 days. They were transported there in less than 1h20, the night before slaughtering and killed by exsanguination

after head-only electrical stunning in compliance with European regulation (EC 1099/2009).

Sample and performance data collection

Samples and performance data were collected throughout the life of the pigs from days 10 to 155. Pigs were weighed on days 10, 28, 29, 31 and 36, to calculate the average daily gains (**ADGs**) between days 10 and 28 ($ADG_{10\text{-}28}$) and between days 29 and 36 ($ADG_{29\text{-}36}$). Bristles were collected from the rump, using an electric hair clipper (Isis, Aesculape, Germany), on days 66 and 148. Blood samples were collected from the jugular vein of individuals using BD Vacutainer 18G (1.2 × 5mm) needles (BD Bioscience, Le Pont de Claix, France). On days 28, 29 and 36, for respectively, 10, 20 and 30 ml blood collection, pigs were gently maintained in a supine position on the knees of one investigator, while on day 66, pigs were nose-snared for a 20 ml blood draw. Blood samples were kept for 1h30 at ambient temperature during transportation. In the laboratory, samples used for whole blood analyses (white blood cell count, flow cytometry, phagocytosis and whole blood assay) were first homogenised on a wheel for 30 minutes. Plasma and serum samples were then obtained after centrifugation for 10 minutes at room temperature at 1 300 and 2 000*g*, respectively, and stored at −80 °C until analysis. At slaughter, the hot carcass weight and lean meat percentage were obtained for all pigs that were still ear-tagged (n = 128/155). The lean meat percentage was calculated based on images obtained at the slaughterhouse from the CSB Image-Meater device (CSB-System AG, Geilenkirchen, Deutschland) as previously described (Blum et al., 2014). All data were collected on both males and females, except blood samples that were collected on males only for practical reasons.

Metabolic parameters' analysis at weaning

Day 28 plasma IGF-1 levels were determined using a Quantikine ELISA kit (Bio-Techne, Noyal-Châtillon/Seiche, France). Serum insulin and plasma glucose concentrations on day 28 were determined using a porcine ELISA kit (Mercodia, Uppsala, Sweden) and a glucose assay kit (Abnova, Taipei, Taiwan), respectively. All measurements were performed on samples collected in the morning on random-fed animals.

Skin and tail lesion scoring

On days 10, 28, 29, 31, 36, and 66, pigs were individually examined to record the number and severity of skin and tail lesions. Skin injuries were scored in four regions (head/neck, shoulder/foreleg, back/ventral and hind/rump) as described: 0 = no lesion; 1 = a single small and superficial lesion (<2 cm); 2 = more than one score 1 lesion or a single red lesion deeper than score 1; 3 = one or more extensive and deep lesion(s) (over 2–5 cm); 4 = a single deep, red and extensive (>5 cm) lesion, or many score 3 lesions; 5 = many score 4 lesions (Calderón Díaz et al., 2014). For each time point, scores for each region were summed up to obtain an overall score per pig. Tail lesions were scored according to Carroll et al. (2018): 0 = intact tail, no sign of bite; 1 = slight or healed lesions, tail tip slightly red; 2 = signs of chewing or puncture without swelling; 3 = signs of chewing or perforation with swelling and possible signs of infection; 4 = partial or total loss of the tail, necrosis. Tails were also inspected the week before departure to the slaughterhouse.

Tail-biting episodes were managed by isolating the biter when identified (for batch 1 only), treating the injured piglets with Repiderma (Schippers, Bédée, France) and Tail guard (Yorkshire Hygiene Solutions, Northallerton, UK) and providing additional enrichment in the pens (hessian sacks, ropes…).

Quantification of stress mediators

On days 28 and 29, serum cortisol and EDTA plasma catecholamine (epinephrine and norepinephrine) levels were measured on samples collected in the morning, using the following kits: Cortisol ELISA (ALPCO, Salem, NH, USA) and 2-CAT (A-N) Research ELISA (LDN, Nordhorn, Germany).

For hair cortisol quantification, we used the protocol described by Heimbürge et al. (2020). Briefly, bristles were washed twice with HPLC isopropanol (Sigma-Aldrich, St Quentin-Fallavier, France), dried at room temperature for at least 2 days and finely cut with scissors. Thirty-five to forty mg of snap-frozen hair were pulverised using 3 mm beads in a Retsch Mixer Mill (MM 400, Verder Scientific, Eragny-sur-Oise, France), and cortisol was subsequently extracted with methanol (Sigma-Aldrich). After centrifugation, supernatants were collected and dehydrated using a vacuum concentrator (Eppendorf, Montesson, France). Dried extracts were resuspended with PBS before quantification using a Cortisol free in Saliva ELISA test (Demeditec Diagnostics GmbH, Kiel, Germany). Finally, cortisol quantity was expressed in pg per mg of hair.

Detection of markers of inflammation

Concentrations of C-Reactive Protein (**CRP**) on days 29 and 36, and haptoglobin on day 66, were quantified in serum by ELISA (Bio-Techne). Circulating endotoxins were quantified on days 29 and 36 in serum with the PyroGene Recombinant Factor C Endotoxin Detection Assay (Lonza, Levallois-Perret. France). Serum IL-6 concentrations were determined on day 29 using a Quantikine ELISA kit (Bio-Techne).

Immune competence assessment

Complete blood cell counts and lymphocyte subpopulations

Complete blood cell counts [total white blood cells, neutrophil, monocyte, lymphocyte and eosinophil counts] were determined on days 29, 36 and 66, from EDTA-treated blood samples using the XT-2000IV analyser (Sysmex, Villepinte, France).

On days 36 and 66, lymphocytes were phenotyped from EDTA-treated blood samples labelled with the following monoclonal antibodies: fluorescein isothiocyanate (**FITC**)-conjugated anti-pig CD4, phycoerythrin (**PE**)-conjugated anti-pig CD21 (both from OriGene, Herford, Germany), PE-conjugated anti-pig CD8 (BD Biosciences) and Alexa Fluor® 405-conjugated anti-pig CD3 (Bio-Techne). Erythrocytes were then lysed (FACS™ lysis, BD Biosciences) according to the manufacturer's instructions. Finally, samples were stained with 1 μM DRAQ5™ fluorescent probe (Thermo Scientific, Courtaboeuf, France) and analysed using a Macsquant flow cytometer (Miltenyi Biotech, Germany). Results were analysed using the FlowJo™ v10 software (FlowJo, Ashland, USA).

Whole blood assay and cytokine concentration measurements

On days 36 and 66, heparinised blood samples were diluted five-fold in RPMI 1640 medium with 2 mM L-glutamine, 100 IU/ml penicillin, and 100 mg/ml streptomycin and stimulated in duplicate using 100 ng/ml O111:B4 *E. coli* lipopolysaccharide (**LPS**) (Sigma-Aldrich). After 18 h incubation at 37 °C and 5% CO_2, supernatants were collected and stored at −80 °C until analysis. Porcine TNFα and IL-8 were quantified by ELISA (Bio-Techne), with detection limits of 31 and 125 pg/ml, respectively.

Phagocytosis test

Ex vivo phagocytosis was assessed on day 36 using the Phagotest™ Kit (BD Biosciences) according to the protocol given by the manufacturer. Briefly, 50 μl of heparinised blood samples were

incubated for 10 min at 37 °C with opsonised FITC-labelled *E. coli* bacteria. Ice-incubated negative controls were included in each experiment. Samples were immediately analysed by flow cytometry using FSC/SSC dot plot to discriminate granulocytes and monocytes. Results were computed using the FlowJo software and expressed as a percentage of phagocytes among monocytes and granulocytes and relative Mean Fluorescence Intensity (**rMFI**, ratio of the mean fluorescence intensity of the positive cells to the negative cells).

Immunoglobulins quantification

The immune response to PCV2 vaccination was assessed on day 66 by quantifying serum anti-PCV2 antibodies (MSD Laboratory, Boxmeer, The Netherlands). Total immunoglobulin G (**IgG**) levels were also determined from day 66 serum using Pig IgG ELISA kit (Fortis Life Sciences, Waltham, USA).

Health status assessment

The farm's health status was rated as "high" according to the annual 2021 & 2022 veterinary records as previously described (Hervé et al., 2022). Indeed, the farm was not exposed to the major swine pathogens. At each visit, we recorded the presence of any clinical signs on each individual and farmers were encouraged to mention any health problem occurring between the visits.

Statistical analyses

Statistical analyses were performed with R (version 4.2.0, RStudio Team (2020)). The main model used the lme4 function of the "lmer" package and included the early-life management mode (conventional vs alternative) as a fixed effect, and the sow (n = 12), the biological mother (n = 35), and the batch (n = 3) as random effects. For analyses at different time points, the age was entered as a fixed effect and the individual as a random effect. Whenever applicable, the sex was added as a fixed effect. The interaction between early-life management and time and/or sex was evaluated.

The ADG was adjusted to the initial weight of the period, *i.e.* the $ADG_{10\text{-}28}$ was adjusted to weight on day 10 while the $ADG_{29\text{-}36}$ was adjusted to weight on day 29. The variables IL-6, insulin, body lesions and tail-biting scores were first analysed as qualitative variables (< or >19 pg/ml for IL-6, < or >2.3 mIU/l for insulin, absence (=0) or presence of body lesions and tail-biting scores >0) using a mixed logistic regression model that included the early-life management as a fixed effect and the sow, the biological mother, and the batch as random effects. For lesion scores, time and sex were added as fixed effects with the individual as a random effect. These variables were subsequently analysed using a linear mixed-effects model as described above.

The goodness of fit of all models (normality of residuals, homogeneity of variance and colinearity) was checked by graphical procedures and Shapiro-Wilk tests. The estimated marginal means (emmeans) and the upper and lower limits of the 95% confidence interval [IC95], calculated using the "emmeans" package, are reported in the text and represented graphically as emmeans [IC95] using GraphPad Prism software (version 9.3.1). Differences were considered significant at $P < 0.05$ and written in bold, while those at $P < 0.1$ were reported as tendencies. When the interaction effect was significant, a Tukey's Honest Significant Difference post-hoc test was performed to search for relevant differences and the results are described in the Results section.

Results

To analyse the consequences of the Alternative A-ELM for pig performance, health, and welfare, we followed different parameters on 80 piglets in comparison to 75 piglets raised under C-ELM. Raw data are provided in Table 1. Of note, in both treatments, the litters were similar in terms of size and mortality rate, including the proportion of crushed piglets. Only the proportion of cross-fostering was different between the two treatments, with 68 and 44% of adopted C-ELM and A-ELM piglets, respectively ($P < 0.01$).

Growth performance

On day 10, the day following early socialisation, no difference in piglets' BW was detected between both groups (A- vs C-ELM) ($P = 0.53$, Fig. 1A). From day 28 to day 36, piglets' BW were not influenced by the ELM ($P = 0.46$) but by the age ($P < 0.001$), with a significant ELMxAge interaction effect ($P < 0.001$). BW significantly increased during this period although we evidenced a transient weight loss the day after weaning in both groups (post-tests $P < 0.01$ for each).

We next compared the average daily gain of the C-ELM and A-ELM piglets before (days 10–28) and after (days 29–36) weaning (Fig. 1B). Before weaning, the ADG was significantly lower for piglets raised under alternative conditions ($P < 0.01$). In contrast, the ADG of the A-ELM piglets was higher in the early postweaning period ($P < 0.001$).

At the slaughterhouse, we collected data from 128 pigs that were still ear-tagged. Early-life management strategies did not affect the hot carcass weight and lean meat percentage at slaughter (data not shown). As expected, sex had a significant effect on the lean meat percentage ($P < 0.01$). Indeed, males displayed a higher percentage of lean meat than females, with respective emmeans of 61.1% [60.4–61.8] vs 60.4% [59.7–61.1].

Metabolism

Plasma IGF-1 levels were not affected by the ELM with an emmean of 106 ng/ml [69.9–142] for C-ELM piglets and 100 ng/ml [64.9–136] in the A-ELM group ($P = 0.76$).

Insulin was detected in 56 out of 74 samples, equally distributed between both treatment groups (odd ratio = 1.38, $P = 0.63$). In these samples, insulin concentrations were not modulated by the ELM ($P = 0.29$).

Glycaemias were significantly lower in the A-ELM group compared to the C-ELM one, with respective emmeans of 1.00 g/l [0.88–1.11] and 1.12 g/l [1.01–1.24] ($P < 0.05$).

Skin and tail lesions

The ELM, and not the age, affected the proportion of animals with body injuries ($P < 0.01$ and $P = 0.08$, respectively), with a significant effect of the interaction (ELMxAge, $P < 0.001$). The day following socialisation, the proportion of animals with body lesions was higher in the A-ELM group as compared to the C-ELM group (45 vs 21%, odd ratio = 3.41[1.53–7.67], post-test: $P < 0.01$) (Fig. 2A). In contrast, after weaning, on day 29, this proportion was higher among the conventionally raised piglets (77 vs 50%, odd ratio = 0.21[0.10–0.47], post-test: $P < 0.001$). Later on, these differences disappeared with similar frequencies of animals presenting body lesions for both treatments on days 36 and 66 ($P = 0.34$ and 0.18, respectively).

Overall, the injuries we observed on the animals were superficial (score < 8). The severity of the body lesions was significantly affected by the age ($P < 0.001$), with no effect of the interaction

Table 1
Raw data of the parameters evaluated in pigs raised under Conventional (C-ELM) and Alternative (A-ELM) Early-Life Management, from birth to slaughter.

Parameters	C-ELM		A-ELM	
	Number	Median [min–max]	Number	Median [min–max]
Performance				
Weight (kg)				
d10	75	3.22 [2.3–5.45]	78	3.53 [2.11–5.39]
d28	74	9.26 [4.49–12.75]	79	8.45 [5.30–11.69]
d29	73	8.76 [4.25–12.44]	80	8.11 [5.24–11.70]
d31	74	9.26 [5.89–13.31]	79	9.09 [4.98–12.24]
d36	74	10.15 [5.60–14.7]	79	10.80 [4.42–14.6]
d66	74	25.5 [16–34]	76	26 [17–34]
Hot carcass weight (kg)				
d155	65	83.8 [64–106.2]	63	82.6 [60.4–99.8]
Lean meat percentage (%)				
d155	65	60.7 [55.4–66.1]	63	61.1 [57.5–63.9]
ADG (g/d)				
ADG_{10-28}	74	324 [114–481]	77	272 [108–411]
ADG_{29-36}	72	243 [−239 to 483]	79	389 [−117 to 739]
Skin and tail lesions[1]				
Severity of skin injuries (score)				
d10	75	n = 16; 1.5 [1–2]	80	n = 36; 1 [1–5]
d29	75	n = 58; 3 [1–8]	80	n = 40; 2 [1–7]
d36	74	n = 41; 2 [1–5]	80	n = 40; 2 [1–5]
d66	74	n = 33; 3 [1–8]	78	n = 26; 2 [1–8]
Severity of tail injuries (score)				
d36	72	n = 7; 1 [1–1]	80	n = 24; 2 [1–4]
d66	74	n = 12; 2.5 [1–4]	78	n = 22; 4 [1–4]
Stress mediators				
Serum cortisol (ng/ml)				
d28	27	80.5 [20.1–143.5]	33	86.9 [19–182]
d29	27	56.7 [23.8–143.7]	33	48.9 [13.8–117.8]
Plasma epinephrine (ng/ml)				
d28	29	0.41 [0.14–1.99]	35	0.46 [0.16–1.39]
d29	29	0.32 [0.14–1.99]	35	0.42 [0.12–1.47]
Plasma norepinephrine (ng/ml)				
d28	20	1.66 [0.51–7.04]	24	1.64 [0.31–4.74]
d29	20	1.42 [0.53–4.97]	24	1.36 [0.32–5.16]
Hair cortisol (pg/mg)				
d66	73	38.41 [24.97–172.06]	72	46.31 [23.78–141.20]
d155	67	52.93 [30–177.63]	67	54.3 [22.4–113.94]
Health status				
CRP (μg/ml)				
d29	34	39.01 [16.05–71.96]	39	51.25 [24.04–121.19]
d36	34	7.41 [1.18–66.45]	36	14.38 [1.96–87.36]
Haptoglobin (μg/ml)				
d66	35	396 [76–1 403]	34	642 [81–2 573]
IL-6 (pg/ml)[2]				
d29	45	n = 12; 30.7 [22.1–96.0]	58	n = 20; 30.9 [19.1–62.5]
Endotoxins (U/ml)				
d29	33	47.1 [16.1–265.1]	36	46.5 [22.1–161.6]
d36	34	29.9 [6.6–197.4]	38	32.8 [7.7–48.0]
Leucocyte counts (10^6/ml)				
Neutrophils				
d29	29	10.64 [1.94–17.69]	37	16.91 [9.90–32.17]
d36	27	6.74 [3.51–14.83]	33	6.67 [2.88–11.56]
d66	32	7.75 [3.23–14.16]	28	7.57 [2.37–19.48]
Lymphocytes				
d29	29	8.62 [1.80–13.38]	37	9.30 [3.49–12.48]
d36	27	9.49 [4.22–17.64]	33	8.69 [4.79–13.57]
d66	32	11.72 [7.26–18.28]	28	10.69 [5.23–19.13]
Monocytes				
d29	29	0.97 [0.38–2.01]	37	1.21 [0.73–2.66]
d36	27	1.06 [0.49–3.13]	33	1.09 [0.64–2.15]
d66	32	1.86 [0.82–2.81]	28	1.77 [0.76–3.53]
Eosinophils				
d29	29	0.15 [0.01–0.53]	37	0.28 [0.05–1.22]
d36	27	0.09 [0.02–0.33]	33	0.16 [0.04–0.37]
d66	32	0.20 [0.04–0.78]	28	0.21 [0.06–0.49]
Lymphocyte subpopulation counts (10^6/ml)				
Cytotoxic T cells				
d36	30	1.58 [0.69–5.67]	37	1.50 [0.53–2.37]
d66	32	2.18 [1.07–4.06]	28	2.22 [0.97–5.97]
γδ T lymphocytes				
d36	30	1.78 [0.56–4.11]	37	1.34 [0.54–3.50]
d66	32	1.90 [0.87–6.03]	28	1.72 [0.79–3.90]

(*continued on next page*)

Table 1 (*continued*)

Parameters	C-ELM		A-ELM	
	Number	Median [min–max]	Number	Median [min–max]
Helper T lymphocytes				
d36	29	2.71 [1.07–4.35]	36	2.52 [1.36–3.88]
d66	30	2.91 [1.67–4.37]	27	2.71 [1.48–5.62]
B lymphocytes				
d36	30	1.61 [0.31–3.18]	38	1.39 [0.70–2.83]
d66	32	1.83 [0.77–7.09]	28	1.27 [0.44–2.53]
Immune parameters				
WBA IL-8 secretion (pg/ml)				
d36	34	1 482 [153–6 239]	38	1 511 [166–5 991]
d66	33	1 985 [304–5 175]	28	2 318 [299–5 125]
WBA TNFα secretion (pg/ml)				
d36	34	257 [53–1 091]	38	257 [71–749]
d66	29	219 [56–1 346]	28	108 [38–890]
Phagocytic capacity				
d36 (% mono-)	21	73.5 [51.7–80.9]	25	77.7 [63.8–84.8]
d36 (% granulo-)	20	86.6 [77.2–94.3]	25	84.9 [73.6–91.6]
d36 (rMFI mono-)	21	14.25 [10.89–20.38]	25	16.1 [12.2–25.48]
d36 (rMFI granulo-)	20	28.93 [19.28–46.3]	25	27.05 [21.05–41.95]
IgG (mg/ml)				
d66	34	5.56 [2.1–20.12]	33	9.05 [1.71–36.46]
PCV2 (a.u.)				
d66	36	10.25 [7.5–11.5]	35	8.9 [6.7–11.4]
Metabolism				
IGF-1 (ng/ml)				
d28	32	98.9 [35.9–198.4]	38	99.5 [20.8–209.0]
Glucose (g/l)				
d28	25	1.17 [0.73–1.45]	27	1.00 [0.75–1.24]
Insulin (mIU/l)[2]				
d28	35	n = 27; 6.0 [3.03–24.93]	39	n = 28; 4.59 [2.48–22.34]

Abbreviations: ADG = Average Daily Gain; CRP = C-Reactive Protein; IGF-1 = Insulin-like Growth Factor-1; IgG = Immunoglobulins G; IL-6 = Interleukin 6; IL-8 = Interleukin 8; PCV2 = type 2 Porcine Circovirus; rMFI = relative Mean Fluorescence Intensity; TNFα = Tumour Necrosis Factor α; WBA = Whole Blood Assay.

[1] For lesions, the number of affected pigs is indicated before the body and tail lesion scores.

[2] For IL-6 and insulin, the number of samples in which the analyte was detected is indicated.

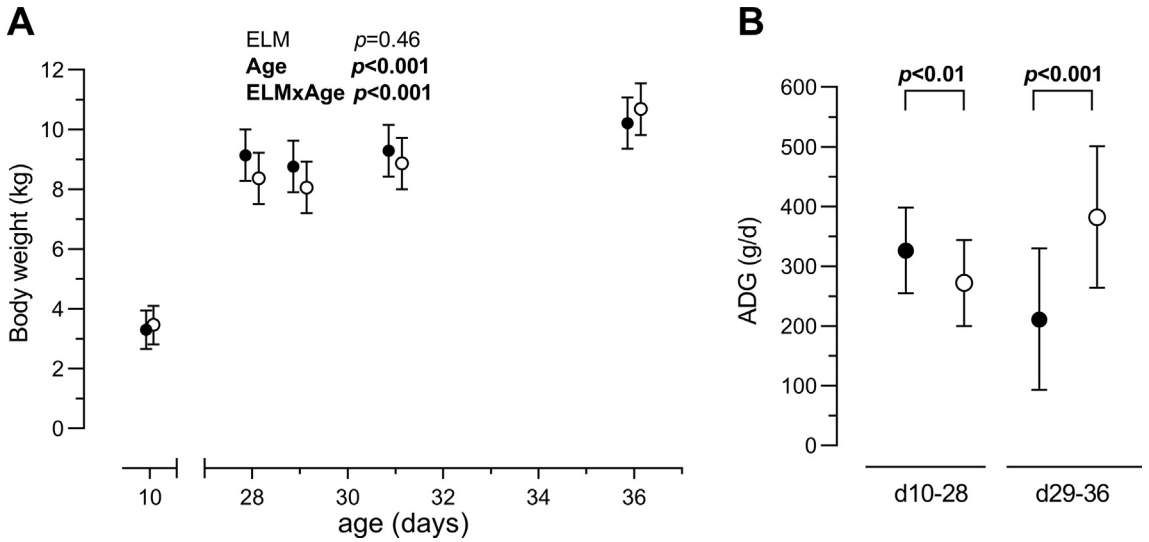

Fig. 1. Performance of pigs reared in C-ELM (black dots) and A-ELM (white dots) conditions. Growth curves (A) and average daily gains during the suckling and the early postweaning period (B). Abbreviations: ADG = average daily gain; A-ELM = Alternative Early-Life Management; C-ELM = Conventional Early-Life Management.

(ELMxAge, $P = 0.10$) (Fig. 2B). Although the early-life management effect was not significant, alternatively raised piglets tended to have less severe lesions than conventional piglets ($P = 0.06$).

Tail-biting outbreaks started during the postweaning period (around day 30 for batch 1 and day 60 for batch 2). On days 36 and 66, early-life management conditions significantly affected the proportion of animals with tail injuries ($P < 0.01$, odd ratio = 0.23[0.09–0.61]) with neither effect of the age ($P = 0.82$) nor of the interaction (ELMxAge, $P = 0.29$). Indeed, this proportion was greater among piglets raised in the alternative system as compared to the control ones on days 36 (30 vs 10%) and 66 (28 vs 16%).

The severity of the tail lesions was also significantly affected by the ELM ($P < 0.001$) but not by the age ($P = 0.42$) with no effect of the interaction (ELMxAge, $P = 0.25$). The A-ELM piglets displayed more severe tail lesions than the C-ELM piglets on day 36 (2.98

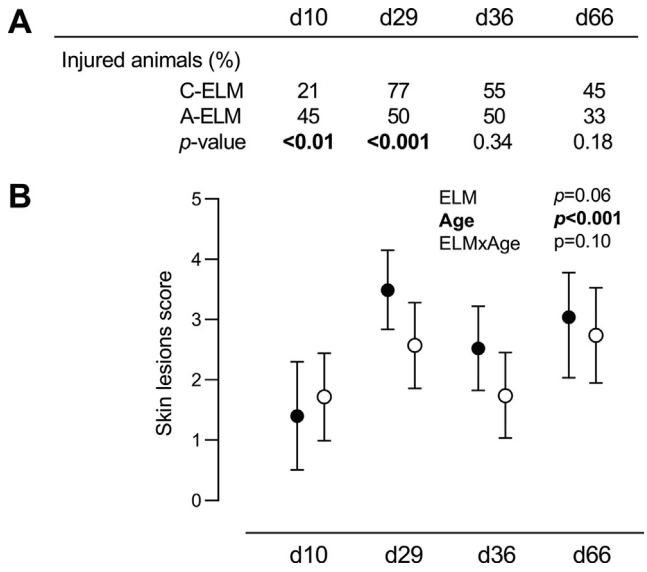

Fig. 2. Body lesions of pigs raised in C-ELM (black dots) and A-ELM conditions (white dots). Frequency of animals displaying body lesions from day 10 to day 66 (A) and severity of the lesions (B). Abbreviations: A-ELM = Alternative Early-Life Management; C-ELM = Conventional Early-Life Management.

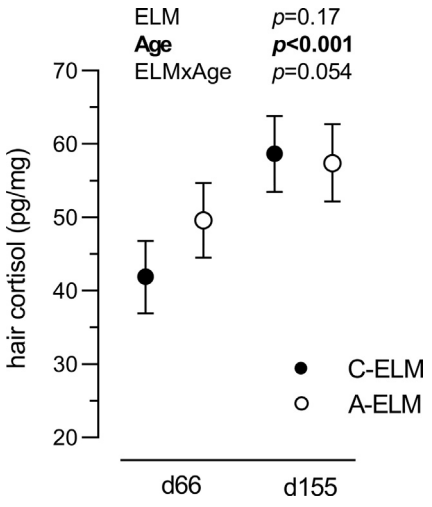

Fig. 3. Hair cortisol in pigs raised in C-ELM (black dots) and A-ELM conditions (white dots). Abbreviations: A-ELM = Alternative Early-Life Management; C-ELM = Conventional Early-Life Management.

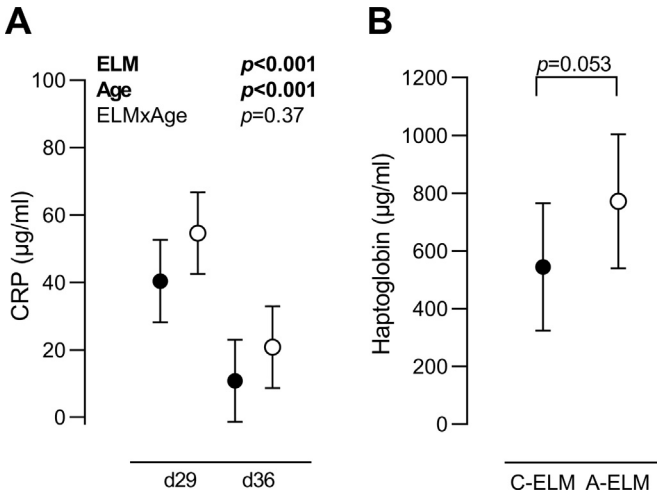

Fig. 4. Serum acute phase protein concentrations in pigs raised in C-ELM (black dots) and A-ELM conditions (white dots). CRP (A) and haptoglobin (B) concentrations. Abbreviations: A-ELM = Alternative Early-Life Management; C-ELM = Conventional Early-Life Management; CRP = C-Reactive Protein.

[1.48–4.48] vs 1.66 [0.10–3.22]), and on day 66 (2.95 [1.58–4.33] vs 2.27 [0.88–3.66]).

At the end of the fattening period, around day 148, sporadic tail lesions were still present in a few pigs of the A-ELM group only (5/80 individuals), with no carcass condemnation at the slaughterhouse.

Stress responses

Emmeans and [IC95] are shown in Supplementary Table S2. Norepinephrine levels were affected neither by the ELM ($P = 0.84$) nor by the age ($P = 0.27$). In contrast, epinephrine levels tended to decrease from day 28 to day 29 ($P = 0.07$), with no effect of the ELM ($P = 0.82$) and the ELMxAge interaction ($P = 0.98$). Cortisolemias also decreased from day 28 to day 29 ($P < 0.001$) while being neither affected by the ELM ($P = 0.70$) nor by the ELMxAge interaction ($P = 0.27$).

Finally, we measured accumulated cortisol in the animals' bristles on days 66 and 155. Hair cortisol levels were not affected by the ELM ($P = 0.17$), but by the age ($P < 0.001$) and tended to be affected by the ELMxAge interaction ($P = 0.054$) (Fig. 3). For both treatments, we observed an increase in hair cortisol levels between days 66 and 155, which tended to be higher in C-ELM piglets.

Inflammatory status

Both the ELM ($P < 0.001$) and the age ($P < 0.001$) affected CRP concentrations, with no interaction (ELMxAge, $P = 0.37$). CRP concentrations were higher in the A-ELM piglets compared to the C-ELM piglets, with a decrease visible from day 29 to day 36 (Fig. 4A). Haptoglobin levels measured on day 66 also tended to be higher in piglets raised under alternative conditions ($P = 0.053$) (Fig. 4B).

We measured serum IL-6 levels on day 29. Since IL-6 was not detectable in some samples, we first analysed this parameter as a qualitative variable and found no effect of the ELM ($P = 0.23$). When detected, the IL-6 levels were not affected by the ELM ($P = 0.37$) with similar concentrations in both treatment groups [emmeans of 38.2 pg/ml [22.8–53.6] for the C-ELM group vs 33.3 pg/ml [21.5–45] for the A-ELM one].

Finally, while endotoxin levels were significantly modulated by the age ($P < 0.001$), they were not affected by the ELM ($P = 0.68$) and the ELMxAge interaction ($P = 0.84$). Endotoxin concentrations decreased between days 29 and 36, with emmeans lessening from 51.0 U/ml [42.3–59.8] to 32.9 U/ml [24.3–41.5].

Immune competence

White blood cell counts

Neutrophil counts were affected by both the ELM ($P < 0.001$) and the age ($P < 0.001$) with a significant interaction ($P < 0.001$). They significantly dropped from day 29 to day 36 in both groups ($P < 0.05$ for both) (Fig. 5A). Interestingly, neutrophil counts were superior in the A-ELM piglets compared to the C-ELM piglets on day 29 ($P < 0.001$).

We found similar results for the eosinophil numbers, with an effect of the ELM ($P < 0.01$) and the age ($P < 0.001$), and a tendency of ELMxAge interaction ($P = 0.071$). As for neutrophils, the

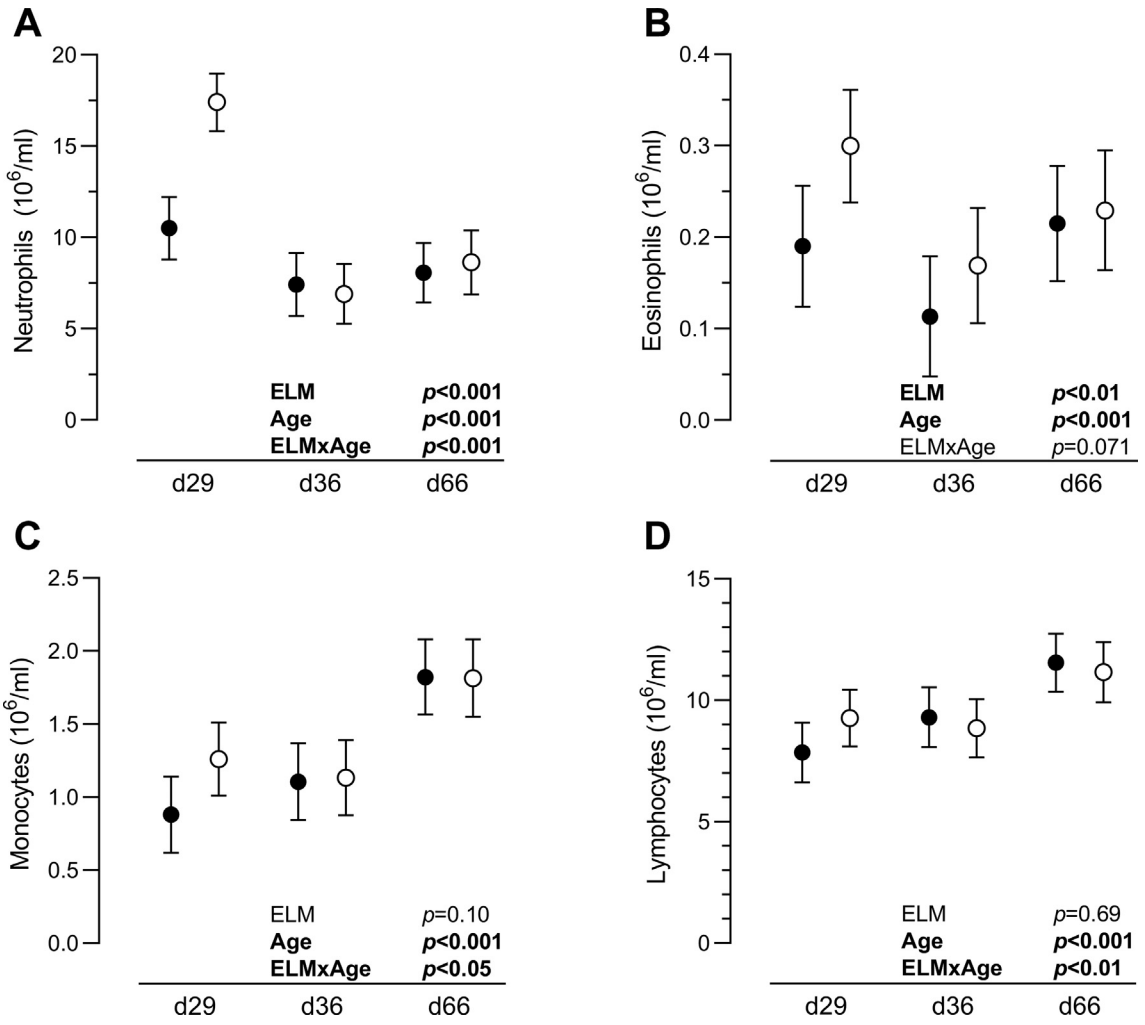

Fig. 5. Leucocyte counts in pigs raised in C-ELM (black dots) and A-ELM conditions (white dots). Neutrophil (A), eosinophil (B), monocyte (C) and lymphocyte (D) numbers. Abbreviations: A-ELM = Alternative Early-Life Management; C-ELM = Conventional Early-Life Management.

eosinophil numbers were higher in the A-ELM piglets on day 29 ($P < 0.05$) (Fig. 5B).

Finally, the monocyte and lymphocyte counts were not influenced by the ELM ($P = 0.10$ and $P = 0.69$, respectively) but by the age ($P < 0.001$) with significant interaction effects (ELMxAge: $P < 0.05$ and $P < 0.01$, respectively) (Fig. 5C and D). On day 29, A-ELM pigs exhibited significantly higher monocyte counts ($P < 0.05$).

In conventionally raised piglets, monocyte and lymphocyte numbers significantly increased between days 29 and 36 ($P < 0.05$) and between days 36 and 66 ($P < 0.001$). In contrast, in A-ELM piglets, both counts were significantly higher only on day 66 ($P < 0.001$).

Lymphocyte subpopulation analyses

The numbers of cytotoxic and γδ T lymphocytes were not affected by the ELM ($P = 0.18$), but they increased significantly from day 36 to day 66 for both treatments (Age: $P < 0.001$, Agex-ELM: $P = 0.83$) (Table 2).

Helper T cell numbers were influenced neither by the ELM ($P = 0.66$) nor by the age ($P = 0.11$).

Finally, the numbers of B cells were influenced by the ELM ($P < 0.05$) but not by the age ($P = 0.77$) with a significant interaction effect ($P < 0.05$). Indeed, on day 66 only, piglets raised under alternative conditions tended to have lower B cell counts than C-ELM piglets (post-test: $P = 0.06$).

Table 2
Numbers of cells in each lymphocyte subpopulation in pigs raised under Conventional (C-ELM) and Alternative (A-ELM) Early-Life Management conditions on days 36 and 66.

Item[1]	C-ELM	A-ELM
Cytotoxic T cells (10^6/ml)		
d36	1.72 [1.18–2.25]	1.46 [0.92–1.99]
d66	2.31 [1.78–2.84]	2.57 [2.03–3.12]
γδ T lymphocytes (10^6/ml)		
d36	1.75 [1.30–2.19]	1.51 [1.07–1.95]
d66	2.07 [1.62–2.51]	1.79 [1.34–2.24]
Helper T lymphocytes (10^6/ml)		
d36	2.73 [2.38–3.08]	2.59 [2.26–2.93]
d66	2.86 [2.51–3.20]	2.86 [2.49–3.23]
B lymphocytes (10^6/ml)		
d36	1.67 [1.24–2.09]	1.52 [1.09–1.95]
d66	1.86 [1.43–2.28]	1.37 [0.94–1.80]

[1] Cytotoxic T ($CD3^+$ $CD4^-$ $CD8^{hi}$), γδ T ($CD3^+$ $CD4^-$ $CD8^{-/med}$), Helper T ($CD3^+$ $CD4^+$) and B ($CD19^+$) lymphocytes were discriminated by flow cytometry, and their numbers were calculated. Emmeans and [IC95] values are reported.

Functional tests

On days 36 and 66, neither the ELM nor the age significantly influenced IL-8 and TNFα production by blood cells after *ex vivo* stimulation by LPS ($P = 0.45$ and $P = 0.16$ for IL-8 and $P = 0.09$ and $P = 0.15$ for TNFα) (Fig. 6A and B). Of note, a significant inter-

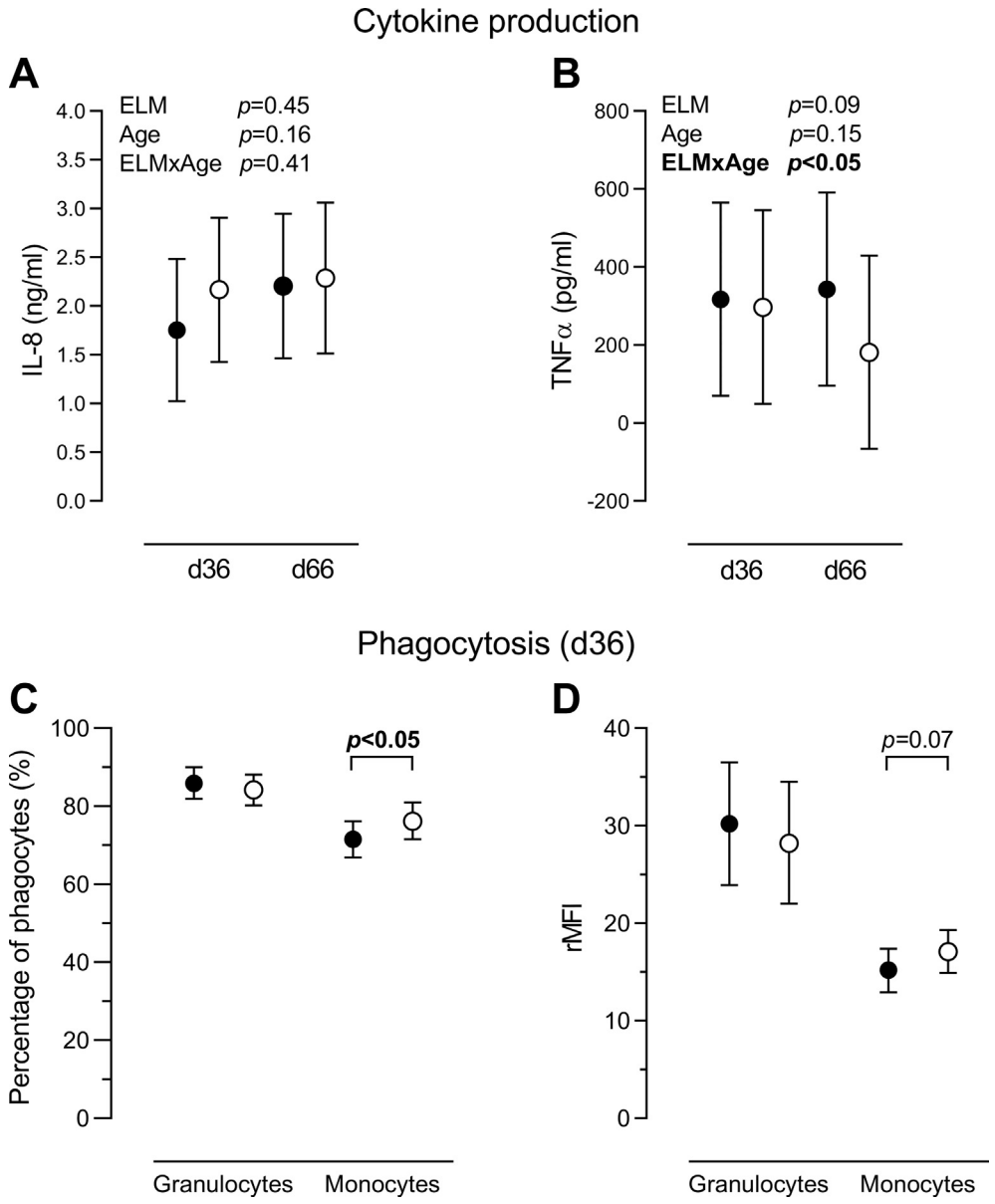

Fig. 6. Cytokine secretion and phagocytic capacity of leucocytes issued from piglets reared in C-ELM (black dots) and A-ELM conditions (white dots). IL−8 (A) and TNFα (B) were measured in response to the *ex vivo* exposure of blood cells to LPS in WBA. Phagocytosis was assessed by flow cytometry. The percentage of phagocytes (C) and rMFI of phagocytes (D) among monocytes and granulocytes are shown. Abbreviations: A-ELM = Alternative Early-Life Management; C-ELM = Conventional Early-Life Management; LPS = lipopolysaccharide; rMFI = relative Mean Fluorescence Intensity; WBA = Whole Blood Assay.

action was observed for TNFα secretion ($P < 0.05$) with a production of TNFα that tended to be lower in the A-ELM piglets compared to C-ELM piglets on day 66 only ($P = 0.092$).

No difference was found in the phagocytosis capacity of granulocytes (percent of phagocytes and rMFI) issued from 36-day-old C-ELM and A-ELM piglets ($P = 0.23$ and $P = 0.25$, respectively) (Fig. 6C and D). Interestingly, the fraction of phagocytes among monocytes was significantly higher in A-ELM compared to C-ELM piglets ($P < 0.05$) (Fig. 6C). Also, the number of bacteria phagocytosed per monocyte, illustrated by the rMFI, tended to be greater in A-ELM piglets ($P = 0.069$) (Fig. 6D).

Serum levels of total immunoglobulins G and anti-type 2 Porcine Circovirus antibodies on day 66

As shown in Fig. 7A, total IgG levels were significantly higher in the A-ELM pigs compared to the C-ELM ones ($P < 0.01$). At the same moment, pigs from both treatments exhibited protective levels of anti-PCV2 antibodies (titers > 7AU) although A-ELM pigs displayed lower titers than C-ELM pigs did ($P < 0.001$) (Fig. 7B).

Health status

In accordance with the health status of the farm, we did not observe any clinical signs suggestive of the major porcine infectious diseases. Concerning locomotor symptoms, we did not detect any ELM effect with, in total, eight cases of lameness and seven cases of arthritis. In addition, 10 piglets developed othematomas and eight hernias, independently of the ELM.

Finally, sporadic cases of diarrhoea were noticed, independently of the ELM (n = 4 on day 28, n = 8 on day 36 and n = 11 on day 66). Of note, on day 66, the difference tended to be significant with two cases in the control group vs nine in the A-ELM one ($P = 0.057$).

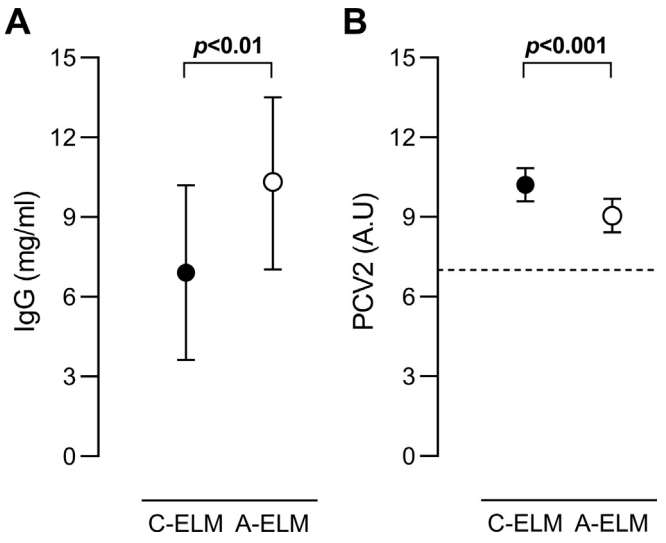

Fig. 7. Serum immunoglobulins in 66-day-old pigs raised in C-ELM (black dots) and A-ELM conditions (white dots). Total IgG concentrations (A) and anti-PCV2 antibody levels (B). The dotted line represents the protective antibody level. Abbreviations: A-ELM = Alternative Early-Life Management; C-ELM = Conventional Early-Life Management; IgG = immunoglobulins G; PCV2 = type 2 Porcine Circovirus.

Discussion

We reported the results of a clinical field study, performed on an indoor, conventional commercial farm with the aim of evaluating whether an improvement of the early-life conditions could help to raise undocked pigs, without affecting the animals' performance, health, and welfare. Indeed, as previously reviewed, early-life conditions, especially during the preweaning period and, to a lesser extent, the early postweaning period, are crucial to a pig's life (Blavi et al., 2021). In our study, alternative early-life management conditions included birth in farrowing pens, socialisation during the lactation period, maintenance of the hierarchical groups at weaning, and delayed transfer to the post-weaning room.

Although we did not detect a significant difference in piglets' BW at weaning, we evidenced that the A-ELM piglets exhibited a lower average daily gain than the C-ELM pigs during the lactation period. A-ELM piglets also displayed lower glycaemia as compared to controls. Although this may result from a lower food intake during the suckling period, it may also be attributed to an increased social activity (playing and fighting). Indeed, one day after the beginning of socialisation, A-ELM piglets showed more body lesions than C-ELM piglets did, although their severity was low. Of note, these lesions were mainly located in the front third of the body, especially on the piglets' heads. At this young age, these lesions may reflect fighting related to teat competition and the establishment of hierarchy (Turner et al., 2006; Salazar et al., 2018).

Later on, alternative early-life management prevented the growth slowdown usually observed after weaning. Hessel et al. already described a positive effect of early socialisation on average daily gain after weaning (Hessel et al., 2006). In our study, early-socialised piglets remained in their social group and did not have to expend energy to establish a novel hierarchy. In agreement, we observed that the percentage of injured animals after weaning was lower in the early-socialised piglets whose lesions were also less severe. These data are in agreement with previous studies that demonstrated the benefits of early co-mingling upon the development of social skills (D'Eath, 2005; Salazar et al., 2018; Camerlink et al., 2018; Ko et al., 2020).

To reduce exposure to stress factors at weaning, A-ELM piglets were also maintained in their home pen for a few more days. Indeed, the weaning period is considered the most stressful period in a pig's life, due to abrupt separation from the sow and transfer to an unknown pen with unfamiliar congeners. Consequently, weaning has been associated with increased circulating cortisol levels (Moeser et al., 2007; van der Meulen et al., 2010). In agreement, in our study, cortisolemia was higher immediately after weaning than the day after. However, we detected no effect of the ELM on circulating levels of stress mediators. Since human handling for blood collection is a strong stressor for piglets, it may have masked a slight difference in cortisolemia between the two treatment groups. To avoid this bias, cortisol could be measured in saliva, which can be collected in a less invasive manner. In these conditions, Salazar et al. evidenced a lower increase in salivary cortisol levels after weaning in presocialised piglets as compared to control pigs (Salazar et al., 2018). To assess long-term stress responses, we measured the hair cortisol concentration, which has been demonstrated to better represent chronic stress than salivary cortisol does (Prims et al., 2019). In our study, although hair cortisol levels increased with age as previously described (Heimbürge et al., 2020), they were poorly affected by early-life management conditions. Thus, the alternative early-life conditions tested here did not reduce individual stress responses.

As recently reviewed, early-life events influence the gut microbiota of piglets with consequences for health and performance (Nowland et al., 2022). For example, early social interactions, by promoting microbial exchanges between piglets, have been shown to alter the composition of faecal microbiota (Bi et al., 2021). Wen et al. described rather positive effects of co-mingling during lactation, with long-term effects on immunity (Wen et al., 2021). We also previously demonstrated that early pathogen exposure affects immunity in piglets (Hervé et al., 2022).

In this study, we compared the immune competence of pigs during the postweaning period. The day after weaning, piglets exhibited high neutrophil counts that may be attributed to the vaccination response. We also found high CRP levels one day after vaccination as previously described (Hernández-Caravaca et al., 2017; Temple et al., 2020). Interestingly, A-ELM pigs displayed more neutrophils and monocytes as well as higher CRP levels than C-ELM pigs, which suggests a stronger response to vaccination of alternatively raised pigs. One week later, monocytes from A-ELM piglets displayed greater phagocytic capacity than control pigs. The eosinophilic pattern after weaning appeared similar to observations made by Juul-Madsen et al. with a nadir at week 6 (Juul-Madsen et al., 2010). The day after weaning, the eosinophil count of the A-ELM pigs was significantly higher than that of the C-ELM pigs. While we cannot rule out that pigs from both treatment groups were not exposed to the same pathogens, the occurrence of clinical signs was low and similar for all piglets at this age. Altogether, these data argue for an enhanced innate immune competence of A-ELM pigs at weaning.

In contrast, on day 66, A-ELM pigs exhibited significantly lower levels of anti-PCV2 antibodies as well as reduced numbers of B lymphocytes, which may reflect an altered cell-mediated immunity. Luo et al. previously described a better specific antibody response in pigs housed in an enriched environment compared to controls (Luo et al., 2020). The vaccination protocol used, which required two injections of the experimental antigen, was performed, far from weaning, starting on day 74. In our study, piglets were vaccinated on day 28, as usually performed on farms. It can be hypothesised that the enhanced innate immune response in A-ELM piglets was detrimental to the setting of the anti-PCV2 response with accelerated clearance of the antigen. Nevertheless, all pigs were effectively protected and total IgG concentrations on day 66 were even greater in A-ELM pigs as compared to the controls.

Despite some positive effects of the alternative early-life conditions on pig growth, body lesions and immune competence during the postweaning period, we recorded more frequent and more severe tail-biting lesions in A-ELM pigs. We provided diverse non-straw enrichment (hessian sacks, metal chains, wood, ropes, etc.), but the diversity and quantity of the enrichments were not sufficient to prevent the occurrence of tail-biting episodes. Although damaging behaviours have been shown to have multifactorial origins, in our case, the main risk factor was raising undocked pigs on a conventional farm. As expected, the increased occurrence of tail biting in A-ELM pigs was associated with higher CRP and haptoglobin levels on day 36 and day 66, respectively, as compared to control pigs. Tail biting is known to induce inflammation in victimised pigs through induction of the acute phase protein response (Heinonen et al., 2010). On day 66, we also observed a higher rate of diarrhoeic pigs in the A-ELM as compared to the C-ELM group, while we do not know whether this was associated with tail biting or not. Indeed, links between poor health and damaging behaviours are thought to be bidirectional (reviewed by Boyle et al., 2022). Tail biting may compromise health especially by favouring the entry of pathogens into open wounds. Conversely, health problems may induce damaging behaviours. For example, induction of a sick behaviour by LPS administration in group-housed gilts has recently been shown to increase the incidence of tail- and ear-directed behaviours (Munsterhjelm et al., 2019).

Lastly, despite tail-biting episodes during the postweaning period, the number of pigs displaying tail lesions was low before departure to the slaughterhouse. Accordingly, there was no carcass condemnation. Also, there was no difference in hot carcass weight and lean meat percentage in pigs from both groups, showing that the overall performance of pigs was similar regardless of their early-life conditions.

Conclusion

The results obtained in this clinical field study suggest that early socialisation, which provides piglets with an enriched environment, could better prepare them to the challenge of weaning. Indeed, piglets reared under improved early-life conditions displayed better growth and immune competence after weaning, with similar performance during the fattening period. However, these results must be treated with care, since in this study, not all piglets were docked and they were housed in different rooms. Thus, other field studies are warranted to evaluate the real benefits and limitations of socialising piglets during the lactation period in intensive farming.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2023.100810.

Ethics approval

The study was carried out in accordance with Directive 2010/63/EU and the Oniris ethics committee for veterinary clinical and epidemiological research approved the experimental protocol (CERVO-2020-22-V). Written informed consent was obtained from the owners for the inclusion of their animals in this study.

Data and model availability statement

Data were not deposited in an official repository. Data and models are available upon request.

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Declaration of interest

None.

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