Applied Animal Behaviour Science 266 (2023) 106022

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

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

Rub 'n' roll – Pigs, *Sus scrofa domesticus*, display rubbing and rolling behaviour when exposed to odours

Maria Vilain Rørvang [a,*], Sarah-Lina Aagaard Schild [b], Anna Wallenbeck [c], Johanna Stenfelt [a], Rebecca Grut [a], Anna Valros [d], Birte L. Nielsen [e]

[a] *Swedish University of Agricultural Sciences (SLU), Dept. Biosystems and Technology, Sundsvägen 16, Box 190, 23422 Lomma, Sweden*
[b] *Innovation Centre for Organic Farming, Agro Food Park 26, 8200 Aarhus N, Denmark*
[c] *Swedish University of Agricultural Sciences (SLU), Dept. Animal Environment and Health, Gråbrödragatan 7, Box 234, 532 23 Skara, Sweden*
[d] *University of Helsinki, Dept. Production Animal Medicine, PL 57 (Koetilantie 2), 00014, Finland*
[e] *The Universities Federation for Animal Welfare (UFAW), Brewhouse Hill, Wheathampstead, Hertfordshire AL4 8AN, United Kingdom*

ARTICLE INFO

Keywords:
Motivation
Olfaction
Scent-rubbing
Sensory behaviour
Skin care
Wallowing

ABSTRACT

Pigs are regarded as having a highly developed sense of smell, although scientific information on the topic is sparse. Here, we describe two behaviours unexpectedly observed in a study assessing pigs' responses to odours and not previously reported in pigs. The study included 192 pigs of commercial breeds, tested in pairs with 12 different odours of non-social origin: 8 essential oils and 4 synthetic perfumes, plus an odourless control. Each odour was tested 24 times in triads of three odours. The results showed that, when exposed to odours, pigs display rubbing and rolling behaviour. Pigs displayed rubbing behaviour in 18 % of all odour exposures. Rolling behaviour was less frequent and displayed 7 times by five different pig pairs. Rubbing was always displayed following sniffing behaviour, and after a rubbing event, the pigs either performed sniffing behaviour (86.1 %), attempts at rolling (8.8 %) or a rolling event (5.1 %). Both males and females performed the rubbing behaviour (61 % female, 39 % male, Wilcoxon signed-rank test: $W = 2199$, $P > 0.1$), rolling behaviour (71 % female, 29 % male) and attempts at rolling (62 % female, 38 % male). Overall, essential oils (lavender, thyme, blood orange, aniseed, cedarwood, cinnamon bark, ginger, and pine) elicited more of the behaviours than the synthetic perfumes (vanilla, musk, apple, and jasmine) or the odourless control. All odours elicited rubbing whereas only four odours (blood orange, ginger, lavender, and pine) elicited rolling. Scent-rubbing/scent-rolling is a well-known behaviour in both wild (e.g., wolves and coyotes) and pet (e.g., cats and dogs) carnivores, although the function is not clear. This is the first report of rubbing and rolling as a response to an odour in pigs. The motivation for performing these behaviours is unknown but may include skin care, comfort behaviour or marking behaviour. Further studies allowing pigs physical access to rub and roll in different odours may elucidate the underlying motivation.

1. Introduction

Pigs are well known for their excellent sense of smell (Pond and Houpt, 1978; Hafez et al., 1962), which they use to explore their surroundings and to forage (White, 1952), to recognise familiar and unfamiliar conspecifics (Kristensen et al., 2001), and to identify and distinguish between individuals (Mendl et al., 2002). However, relatively few studies on porcine olfaction are available, and these mainly focus on studying aspects relevant for increasing the output from commercial pig production. One such example is optimising reproduction, where boar odour or androsterone may be utilised to stimulate oestrus in sows (e.g., Rekwot et al., 2001; McGlone et al., 2019a, 2019b). Studies have also focussed on how sow pheromone(s) may be involved in piglet udder detection (e.g., Morrow-Tesch and McGlone, 1990a, 1990b).

When pigs explore their olfactory environment, they direct their snout towards the odour, and sniff the air near the source to allow their olfactory organ to detect volatile odorants (Pond and Houpt, 1978; Schild and Rørvang, 2023). While the olfactory epithelium lining the nasal cavity can detect the volatile molecules, the vomeronasal organ relies on direct contact or close proximity to detect less volatile

* Correspondence to: Swedish University of Agricultural Sciences (SLU), Dept. Biosystems and Technology, Box 190, 234 22 Lomma, Sweden.
E-mail address: Mariav.rorvang@slu.se (M.V. Rørvang).

https://doi.org/10.1016/j.applanim.2023.106022
Received 24 May 2023; Received in revised form 24 July 2023; Accepted 26 July 2023
Available online 28 July 2023

molecules (for detailed review see: Schild and Rørvang, 2023). Sniffing is a well-known part of pig exploratory behaviour (Studnitz et al., 2007), and an innate part of pigs' behavioural repertoire with pigs having functional olfactory ability in utero (Guiraudie-Capraz et al., 2005). Sniffing is seen whilst rooting, as pigs will use their snouts both to sniff and root in a substrate to locate edible parts, and to satisfy a motivation to explore (termed inquisitive exploration; (Day et al., 1995; Wood-Gush and Vestergaard, 1989)). Pigs display avoidance behaviour when exposed to certain odours, such as ammonia, indicating aversion (Jones et al., 2001). However, the responses of pigs to non-aversive odours remain poorly understood, and odour exploration behaviour of pigs has not been described in detail, over and above the frequency and duration of sniffing.

Here, we describe two behaviours not previously reported in pigs when exposed to odours. These behaviours were unexpectedly observed in a study assessing the responses of growing pigs to odours of non-social origin.

2. Materials and methods

The first occurrence of the novel behaviours described in Table 1 were observed in the video material collected for another study (Rørvang et al., 2023) investigating pigs' interest in odours of non-social origin. A detailed description of the novel behaviours and the collection of data were therefore carried out as a post hoc analysis of this video material. An extensive description of all materials and methods can be found in Rørvang et al. (2023).

2.1. Experimental venue

The study was conducted at the Swedish Research Center Lövsta, in Uppsala, Sweden. The tests were carried out over a period of 5 months, starting in February 2022.

2.2. Ethical note

Prior to the start of the experiment, the procedures and details of the experiment were evaluated by the Board of Ethical use of Animals in Teaching and Research, Swedish University of Agricultural Sciences, Uppsala, Sweden, and an ethical permit was obtained from the Swedish Board of Agriculture, Uppsala, Sweden ID number: 5.2.18–02900/2020. As part of the ethical permit, humane endpoints were defined prior to the study, in collaboration with the veterinarian, and the head of research on the research farm, who both agreed to the procedures used in the study. All procedures were conducted in accordance with the ethical guidelines proposed by the Ethical Committee of the ISAE (International Society of Applied Ethology) (Sherwin et al., 2003) and met the ARRIVE guidelines (Kilkenny et al., 2010). As the experiment was conducted during the COVID-19 pandemic, measures were taken to comply with the current precautions during the period October 2021 – June 2022. The experiment was conducted in Sweden, and hence complied with the Swedish COVID-19 regulations as of February 22nd, 2022.

Table 1
Ethogram of the focus behaviours: Rubbing and rolling, and behaviours (other than rubbing or rolling) preceding and following an event of either rubbing or rolling when pigs were exposed to odours of non-social origin.

Behaviour	*Description*
Rubbing	The pig rubs or scratches its head, neck and/or side/flank on the pen fixture near the odour (i.e. with the head less than 50 cm away from the odour, and without sniffing another odour insertion point, Fig. 4). The rubbing events may include one sequence of repeated rubs, or several repeated sequences of rubbing i.e. repeated rubbing, a short pause (often including sniffing of the odour), and immediately another sequence of repeated rubbing (Supplementary Video S1)
Rolling/attempt at rolling	The pig lies down in a flopping movement (abrupt flopping onto either side of the body). The behaviour may include repeated wagging or rubbing of the body while lying on the left or right side, i.e. repeated rolling (Supplementary Video S2), or only flopping once onto the side i.e. attempts at rolling (Supplementary Video S3)
Sniffing	The snout of the pig is in close proximity to the odour (i.e. less than the length of a pig snout ~8 cm) away from the odour insertion point (Fig. 4)
Walk away	The pig moves at least two steps away from the odour
Other	None of the above.

2.3. Animals, test pens and odours

Growing pigs (n = 192) of domestic breeds participated in the study. The sample size was based on Rørvang et al. (2017) including at least 24 animals for every three odours tested. Hence, the study needed to include at least 96 pigs in order to test 12 odours (see section "Odours" below). To limit the amount of stress related to social isolation, pigs were tested in pairs, and thus the total sample size was 192 pigs (96 pairs). This resulted in 24 replicates per odour (24 tests of each odour on a total of 48 pigs/24 pig pairs). The majority of the pigs (n = 149) were crossbred Hampshire and Yorkshire, 35 were crossbred Hampshire and Landrace, and 8 were crossbred Yorkshire and Duroc. The pigs were tested in the current experiment when they were on average 12 weeks old (median: 96 days old, 25–75 % quartile range: 88–104 days old), and weighed on average 64.9 kg (SE = 1.0 kg). Breed and age of the pigs were based on availability on the research centre as the study used the pigs bred and kept at the research centre (The Swedish Livestock Research Centre, 2017). All pigs were moved from their home pens and placed into identical pens in the test room in littermate pairs of one female and one male. Details of the odour testing set-up can be found in Rørvang et al. (2023) but, briefly, the test pens had two circular odour insertion points (Ø: 14 cm; 55 cm apart) drilled through the front wall of the pen each fortified with a metal ring (Fig. 1B). These two odour insertion points were used to present the test pair with an odourless control and an odour during the tests (Fig. 1C), balanced for side. The size of the odour insertion point allowed the pig to insert the snout into the hole and to open the mouth slightly but not fully. This prevented the pigs from getting into physical contact with the odour samples (see below, and Fig. 1C), while also allowing both the main and accessory olfactory organs to detect the odours (Schild and Rørvang, 2023).

Twelve odours were selected for the tests. The choice was based on the limited existing knowledge on odour interest in pigs (Nowicki et al., 2015; Oostindjer et al., 2011; Van de Weerd et al., 2003) and the chemical information for each odour used (avoiding toxicity and irritability) and all were approved for human use. All odours were oil-based, eight were essential oils and four synthetic perfumes. Essential oils are derived from 100 % natural sources, whereas synthetic perfume oils are a blend of both natural and nature-identical odorant molecules (Rørvang et al., 2023). The odours were not diluted, and 6 drops of odour was dispensed using the built-in drip function in the odour bottles containing each odour (Fig. 2) to standardise the amount of each odour. The odour drops were added onto a filter paper, which was fastened to the bottom of a plastic (polypropylene) container (L x W x H: 21 cm × 15 cm × 17 cm; Fig. 2). This placement of the filter paper allowed the pigs to sniff but not physically touch the filter paper or the odour, to avoid mixing taste and smell and to prevent contamination of the pigs (Fig. 3). The twelve odours were grouped together in four triads of odours, where each of the three odours were of different origin (herb, spice, from a tree, root, fruit, flower, seed, or mixture): A) **vanilla**, aniseed, and blood orange; B) **musk**, **apple**, and cinnamon bark; C) ginger, pine, and **jasmine**; and D) cedarwood, thyme, and lavender (odours in bold were the synthetic perfumes) (see supplementary Table S1 for full details of odours). Each pig pair was tested only once to limit the risk of sniffing fatigue or loss of motivation to explore the odours, as the test paradigm relied on spontaneous investigation of the

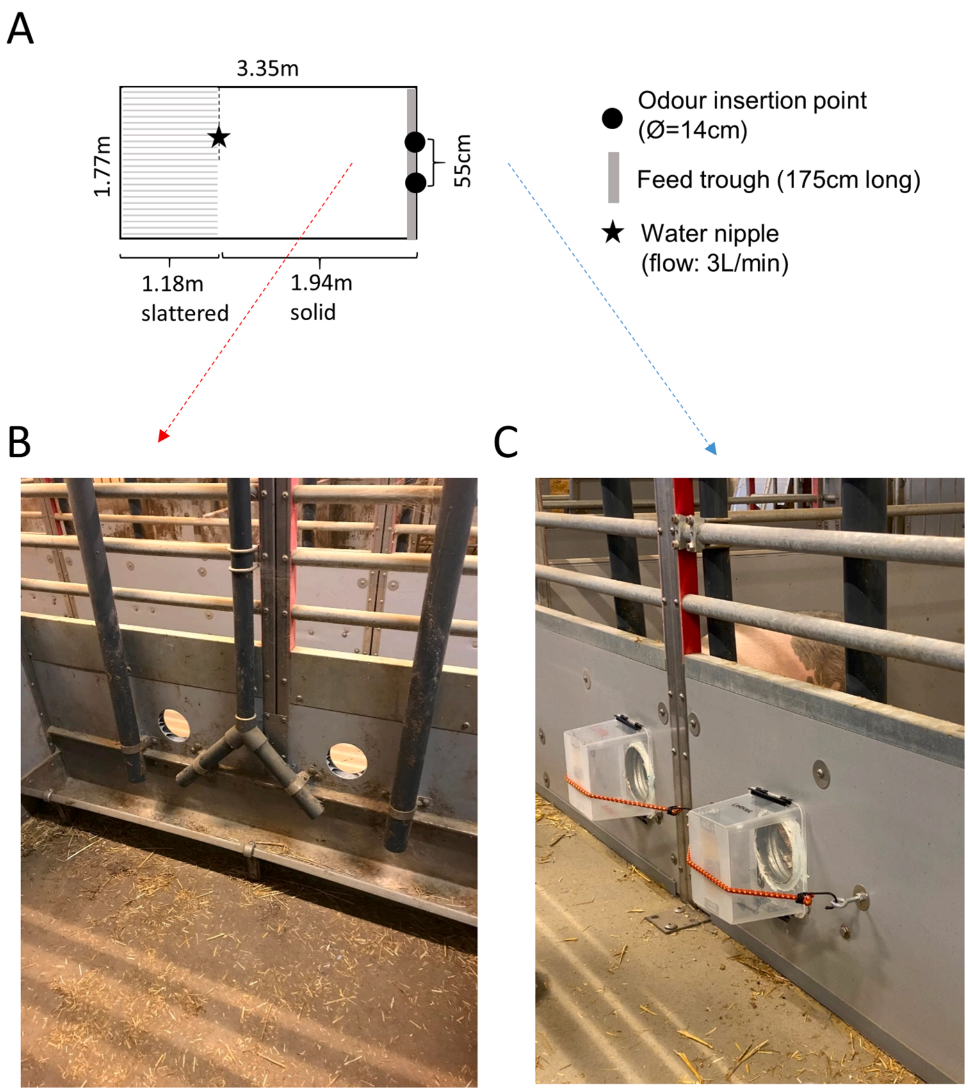

Fig. 1. Overview of the experimental pen. A) Schematic top view of the test pen, with dimensions indicated. The placement of the water nipple, the feed trough and odour insertion points are highlighted. B) The two odour insertion points seen from within the test pen (indicated by red dashed arrow). The odour insertion points were holes drilled through the front pen fixture over the feed trough, 19 cm above floor level. C) The odour insertion points seen from outside the test pen (indicated by blue dashed arrow) during a test, where the odour insertion points are covered by the odour container, one containing an odour, and one containing an odourless control. The containers containing either an odour or control were fastened by the orange elastic strap with hooks on both ends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

odours. Each pig pair was randomly assigned to a group of three odours (A, B, C, or D) prior to testing. On each test day, only one set of three odours was tested in the experimental building, to prevent other pigs in the building being exposed to their odour triad prior to being tested.

Fresh odour samples were prepared in the morning on each test day, in a separate room away from the pigs. An odourless control consisting of demineralised water was also prepared. All samples were contained in closed plastic containers, which were not opened until the specific odour samples were to be tested (Figs. 2 and 3). Each odour and odourless control was prepared in one distinct container, and these containers were kept apart to avoid contamination.

2.4. Test procedure and paradigm

The test paradigm was similar to the Habituation/Dishabituation test paradigm used to study olfactory abilities in a variety of species (e.g. rats: Sundberg et al., 1982, mice: Yang and Crawley, 2009, cattle: Rørvang et al., 2017, horses: Hothersall et al., 2010, pigs: Mendl et al., 2002). Three trained experimenters performed the tests. These experimenters positioned (and removed) the odour and control sample containers over the odour insertion points with the containers each covering the entire odour hole (Fig. 3). Each odour and control were presented three times in a row with 2-minute breaks in between odour exposures. Each odour exposure lasted 1 min, and after the third odour exposure, a new odour was presented in the same manner (i.e. 9 odour exposures for each pig pair in total, 3 exposures of each odour in the triad). Pigs were free to engage in any activities during testing. The total duration of each test for each pair was 25 min (i.e. 9 one-minute exposures separated by 8 two-minute breaks), and total duration each group of pigs were in the testing facility was 2–3 days depending on litter group size. Each odour and control sample container was removed entirely from the odour insertion points during the breaks, and the containers were covered up with their respective airtight lid (containers and lids were labelled to ensure no lids were mixed).

All tests were video recorded using four GoPro Hero 9 (one filming each experimental pen, Fig. 4), and behavioural observations were subsequently carried out, using continuous ad-libitum sampling. Rubbing behaviour, rolling attempts, and rolling behaviour were discovered during these observations. The behaviours were thus subsequently described in detail, and behaviour sampling (Bateson and Martin, 2021) was used to record rubbing and rolling behaviour during each 1-min odour exposure, as well as the immediate behaviour preceding and following each rubbing and rolling event. Duration of rubbing and rolling behaviour was timed (in seconds) and summed for each pig pair, and frequency of each behavioural event was counted at pair level. Although the experimental unit was the pig pair, it was noted which individual performed the behaviour to allow potential effects of sex and age to be considered (Fig. 4). The behaviour of the focal pig (determined

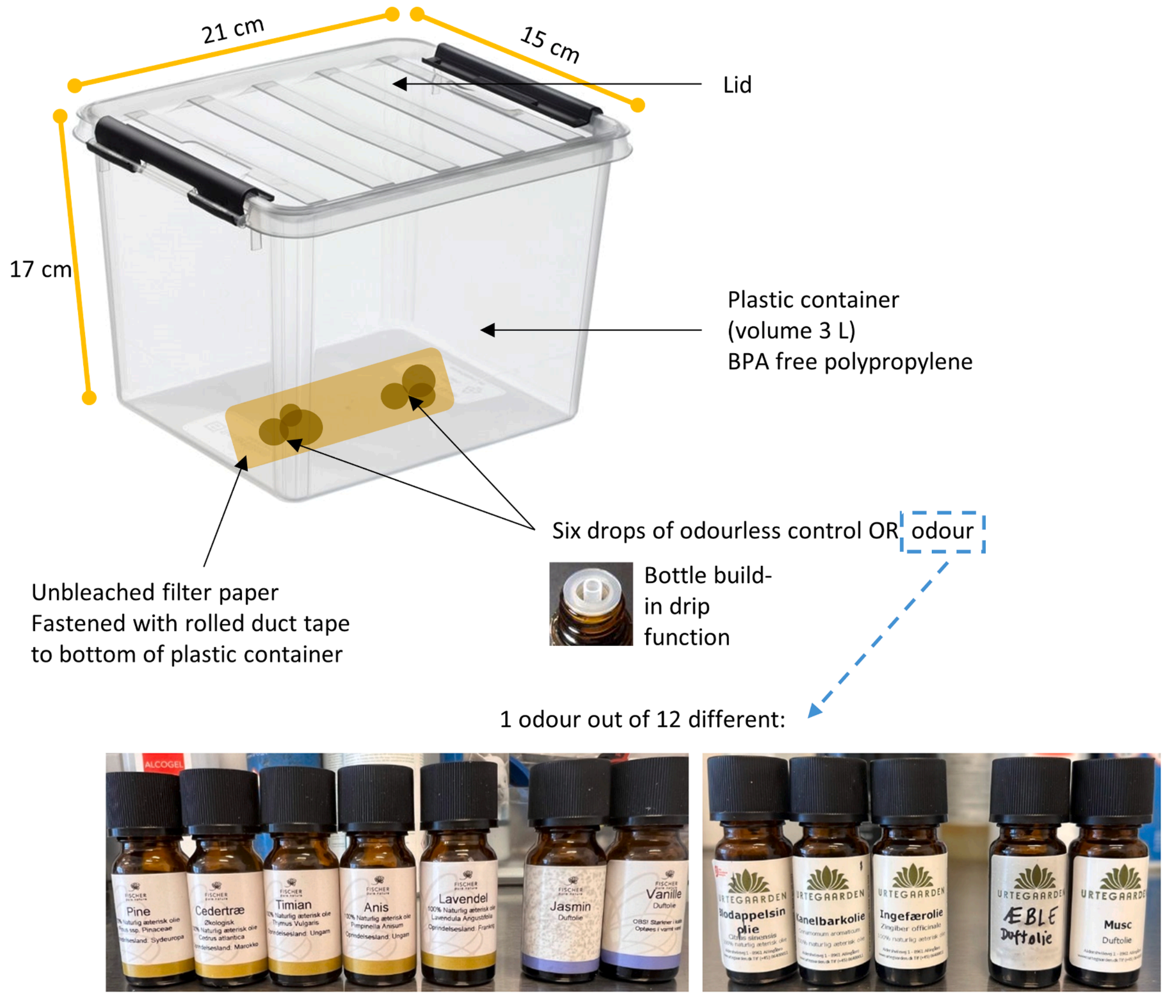

Fig. 2. A schematic view of the odour sample preparation performed in a separate room distanced and closed off from the pigs. The plastic container (3 L) with corresponding lid is shown, and the placement of filter paper containing the absorbed 6 drops of either an odour (all 12 odours are shown) or an odourless control (demineralised water) is illustrated. The build-in drip function in each odour bottle is also illustrated, which ensured a standardised amount of odour on each sample.

post hoc based on whether they performed the focus behaviour or not) preceding and following the focus behaviour event (i.e. before and after rubbing, rolling and rolling attempts) was also recorded using the ethogram in Table 1. The behaviours were extracted by an experienced observer, who was not involved in the tests, and thus blind to which specific odour was presented, although not blind to which side (left or right) had the odour/control.

2.5. Data and analyses

The data consisted of nine odour exposures for each pig pair, and thus the total data set comprised 864 odour exposures. Out of these, 90 exposures were lost due to camera error or power failure, leaving 774 odour exposures for analysis. Due to the relatively low occurrence of the rubbing and rolling behaviour, data were analysed using statistical tests applicable to non-normal data (right skewed data due to high amount of zero's). When comparing data on essential oils and data on synthetic perfumes Wilcoxon signed-rank tests were used. Data of each specific odour were compared using the Dunn Kruskal Wallis multiple pairwise comparisons. Due to low occurrence of rolling behaviour, only data on rubbing were analysed for potential effects of sex and age: potential effects of sex were analysed in a Wilcoxon signed-rank test comparing females and males, and potential effects of age were analysed in a Spearman Rank correlation. Statistical analysis of the potential effects of breed were not possible due to the skewed distribution of breeds (e.g. 149 out of 192 pigs were Yorkshire x Hampshire crosses). Statistical significance was considered as $P < 0.05$, and all statistical procedures were performed in R (version 4.1.0. (R-Core-Team, 2022)), using the interface R-studio (version 2022.07.1, build 554 (R-studio Team, 2022)), and R-package FSA (Ogle et al., 2023). For graphical illustrations, we additionally used R-package ggplot2 (Wickham, 2009), and Microsoft Power point 2016.

3. Results

Odours eliciting the most rubbing and rolling behaviour were essential oils: lavender, thyme, ginger, pine, cedarwood, blood orange, aniseed, and cinnamon bark, whereas the synthetic perfumes: apple, musk, vanilla, and jasmine elicited the least, and the control (demineralised water) elicited none of the focus behaviours (Table 2).

3.1. Rubbing behaviour

Pigs displayed rubbing behaviour in 137 of the 774 odour exposures (18 %). Repeated sequences of rubbing were predominant (Video S2), although single occurrences of the behaviour were also observed. Due to the low number of single occurrences of rubbing observed, all rubbing events were summed prior to analyses. Rubbing behaviour was displayed by 51 of the 96 pig pairs, and a rubbing event on average lasted 7 s. Both males and females performed the behaviour (61 % female, 39

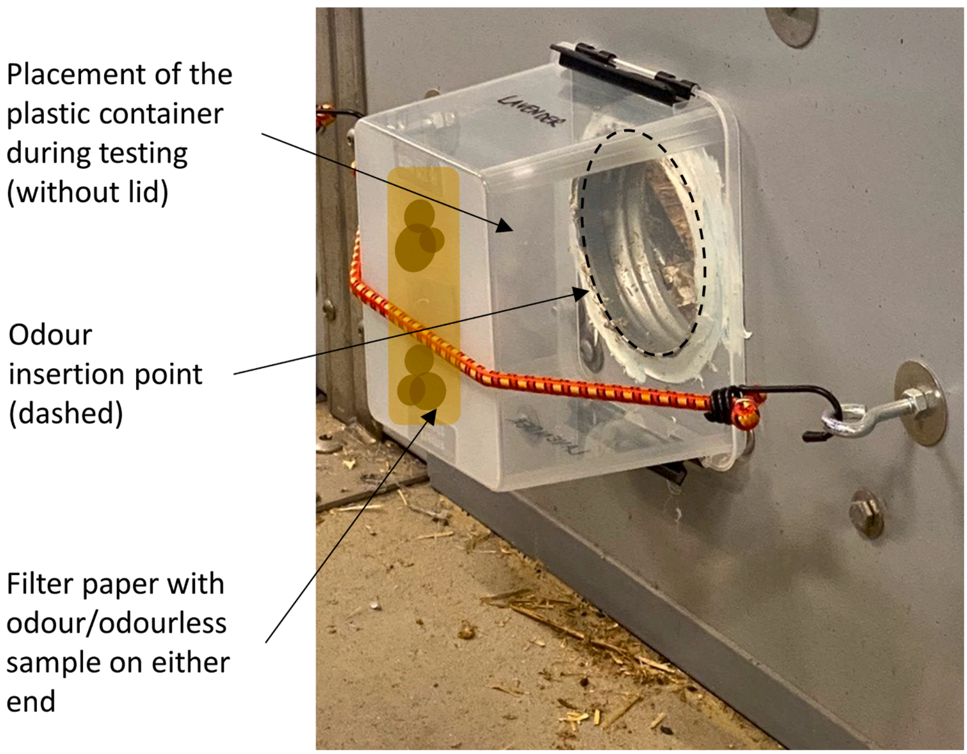

Fig. 3. Illustration of the placement of the plastic container during testing. The plastic container, containing either an odour or an odourless control, was placed without lid on the odour insertion point (black dashed circle), covering the entire hole. The filter paper containing the odour or odourless sample was attached to the bottom of the plastic container (brown markings inside the plastic container). This arrangement ensured that the sample was placed in front of the pig snout while the pig was sniffing inside the odours insertion point, as that the pig could not physically touch the sample in order to avoid mixing taste and smell.

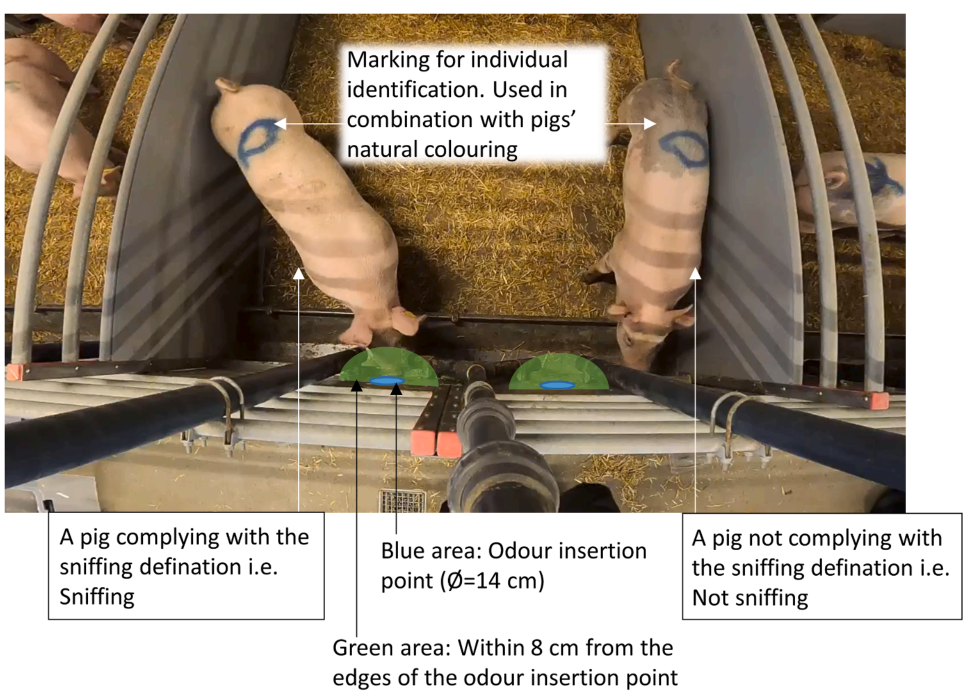

Fig. 4. Top view of a pig pen during testing. In the bottom of the picture, the odours insertion points are given (blue circles 55 cm apart), and the corresponding area around each point (green), illustrates the sniffing definition (snout within 8 cm from the edges of the odours insertion point). Inside the pen, the pig to the left illustrates a pig that is complying with the definition of sniffing, and to the right a pig that is not complying i.e., not sniffing. Both pigs are marked with individual identification (sprayed mark in combination with the pigs' natural colouring). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

% male, Wilcoxon signed-rank test: W = 2199, $P > 0.1$) and there was no significant effect of age (Spearman Rank Correlation, $r^2 = -0006$, $P > 0.1$). Due to the skewed distribution of the breeds (see above), no statistical analysis was carried out, but rubbing was performed by all the breeds. Rubbing was always displayed following sniffing behaviour, and after a rubbing event, the pigs either performed sniffing behaviour (86.1 %), attempts at rolling (8.8 %) or a rolling event (5.1 %). All odours elicited rubbing, but rubbing was least frequent when pigs were exposed to vanilla, and most frequent when pigs were exposed to pine and ginger (Fig. 5B, Dunn Kruskal Wallis pairwise comparisons: $P < 0.01$). The average duration of a rubbing event was significantly higher for aniseed compared to vanilla and cedarwood, whereas none of the other odours differed significantly (Fig. 5A).

Supplementary material related to this article can be found online at doi:10.1016/j.applanim.2023.106022.

Table 2
Frequency (number of events per test) and total duration (s) of rubbing and rolling, and frequency of rolling attempts for essential oils and synthetic perfumes (Mean ± SE).

Odour type	*Rubbing frequency*	*Rubbing duration*	*Rolling frequency*	*Rolling duration*	*Rolling attempts (frequency)*
Essential oil (n = 8)	0.46 ± 0.050	1.38 ± 0.18	0.017 ± 0.0068	0.064 ± 0.028	0.034 ± 0.0092
Synthetic perfume (n = 4)	0.28 ± 0.057	0.96 ± 0.23	0.00 ± 0.00	0.00 ± 0.00	0.0039 ± 0.0039
P[a]	0.008	0.010	0.064	0.064	0.023

[a] From Wilcoxon signed-rank test.

3.2. *Rolling behaviour and attempts at rolling*

Rolling behaviour was less frequent than rubbing behaviour (Fig. 5C and D), and was displayed 7 times by five different pig pairs. As a result, no statistical analysis was performed due to low power. A repeated rolling event lasted on average 4.9 s (see Fig. 5C for details per odour). Rolling behaviour was displayed by both males and females (71 % female, 29 % male), and was always preceded by a rubbing event.

Attempts at rolling were displayed 19 times by 15 different pig pairs (including the five pig pairs who also performed rolling behaviour) (Fig. 6). Attempts at rolling were displayed by both males and females (62 % female, 38 % male), and were preceded by either sniffing the odour, or rubbing behaviour. After an event of rolling, or an attempt at rolling, the pig would always go back to sniffing the odour. Due to the low occurrence of rolling behaviour and attempts at rolling (Figs. 5C, D and 6) statistical analysis of potential age and breed effects were not performed, but rolling was restricted to Yorkshire x Hampshire crosses, which is likely confounded with the relatively large proportion of the pigs (149 out of 192) being this particular cross.

4. Discussion

This study is the first to describe rubbing and rolling behaviour in pigs as a response to sniffing odours of non-social origin. Rubbing and rolling were observed when the pigs were exposed to the odours, and never in response to the odourless control. Rubbing behaviour was observed after the pig had sniffed the odour and was found with all odours tested. Rubbing behaviour was also the behaviour preceding both rolling behaviour and attempts at rolling. Rolling behaviour and attempts at rolling were less frequent than rubbing, and were always

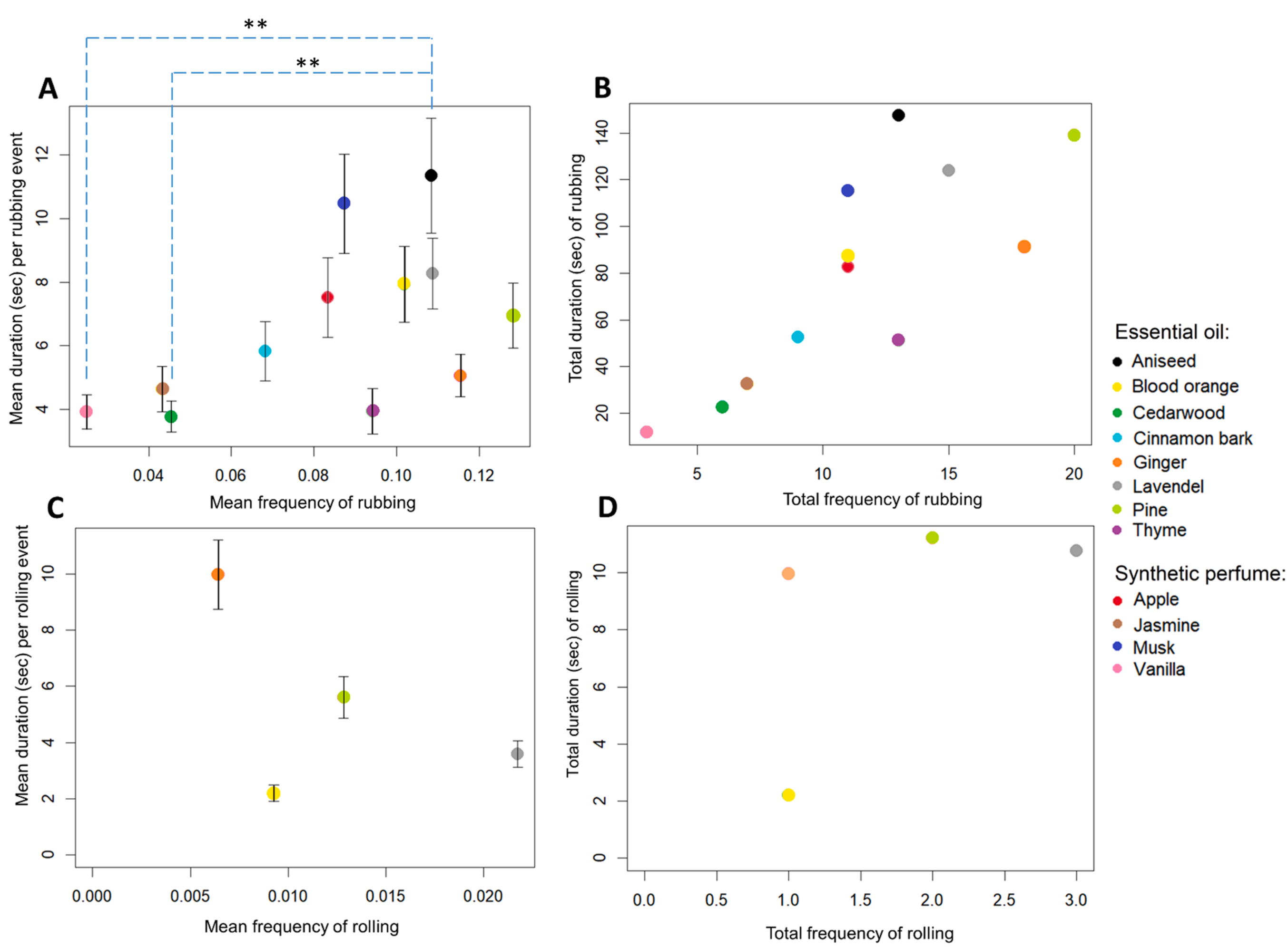

Fig. 5. Rubbing and rolling behaviour when exposed to the odours. A) Mean duration (seconds) of each rubbing behaviour event during exposure to the specific odours, and mean frequency of rubbing behaviour over the total number of tests. The significance given is based on Dunn Kruskal Wallis multiple pairwise comparisons (aniseed mean duration per behaviour event is significantly higher than vanilla and cedarwood). B) Total duration (seconds) of rubbing behaviour during exposure to the specific odours, and total frequency of the behaviour. C) Mean duration (seconds) of each rolling behaviour event during exposure to the specific odours, and mean frequency of the rolling behaviour over the total number of tests. D) Total duration (seconds) of rolling behaviour during exposure to the specific odours, and total frequency of rolling. Error bars indicate ± SE, and essential oils and synthetic perfumes are indicated with specific colours. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

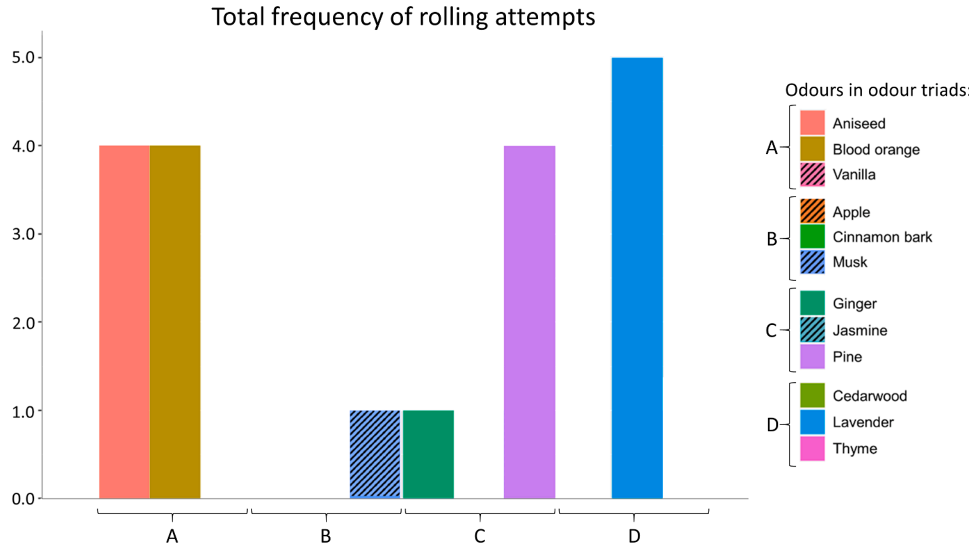

Fig. 6. Rolling attempts. Total frequency of rolling attempts during exposure to each specific odour, grouped into the triads in which they were tested. Synthetic perfumes (apple, jasmine, musk and vanilla) are dashed. No statistics performed due to low occurrence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

followed by the pig sniffing the odour again.

Rubbing and rolling behaviours as a response to an odour are well-known in companion animals such as dogs and cats (Hepper and Wells, 2017; Lee et al., 2010), but have never, to our knowledge, been described in domestic pigs as a response to odours before. Some anecdotal observations of rubbing in free-range pigs are mentioned in the literature. Stolba and Woodgush (1989) observed pigs housed in semi-natural environments back in 1989, and noted that pigs rubbed themselves against certain trees located within 3–25 m from their nest. Concurrently, in a study of free-range lactating sows, Jakobsen (2018) saw more rubbing behaviour in sows with access to poplar trees compared to sows housed in paddocks without trees. In 2011, Bracke (2011) also mentioned scratching and rubbing but in relation to pig skin care. According to Bracke (2011), wallowing is linked to scratching and rubbing, as these behaviours are followed by wallowing when pigs attempt to remove dried mud or ectoparasites (Dickson et al., 2001). Wallowing in mud is a well-documented behaviour in pigs, serving a thermoregulatory purpose as pigs display more wallowing at increasing temperatures (e.g., Ingram, 1965; Huynh et al., 2005), and is commonly seen in connection with skin care (e.g., Fraser, 1970; McMillan et al., 2000). None of the mentioned studies, however, report these behaviours in relation to odours. Bracke (2011) mentions a possible relation between ungulate scent-rubbing and wallowing, in the form of wallowing in mud which has a smell due to decomposing organic materials in the vet soil, but this theory has yet to be confirmed. In our study, rubbing appeared to be elicited by sniffing the odour, and some pigs subsequently displayed rolling behaviour (or attempts at rolling), which was always followed by the pig sniffing the odour (again), which in turn elicited another display of either rubbing behaviour, rolling behaviour or attempt at rolling. Hence, although wallowing and rolling behaviour share a certain level of resemblance, the behaviours may serve different functions.

In studies of commercially housed pigs, there is mentioning of rubbing interpreted as a comfort behaviour, and rolling interpreted as a play behaviour (Bolhuis et al., 2005, 2006; Ocepek et al., 2020) in connection with rooting material. Bolhuis et al., (2005, 2006) defined rubbing as scratching the body against objects or pen mates, and this definition shares semblance with the defined rubbing behaviour in this study. However, the rubbing behaviour observed in Bolhuis et al., (2005, 2006) was not linked to an odour or sniffing behaviour. In the aforementioned studies, rolling was defined as movements from side to side while lying on the back or the side. In comparison, rolling was in this study defined as the pig flopping onto one side of the body, followed by repeated wagging or rubbing of the body while lying on the side (i.e. no changing of sides). Hence, the play related rolling behaviour described in Bolhuis et al., (2005, 2006) and Ocepek et al. (2020) differs from the rolling behaviour observed in this study. It is, however, possible that the pigs in this study could have performed a type of rolling behaviour more comparable to play rolling if they had physical access to the odours, or if the odours had been presented on rooting material. On that note, the rolling behaviour observed in Bolhuis et al., (2005, 2006) and Ocepek et al. (2020) and the rubbing behaviour noted in Bolhuis et al., (2005, 2006) could be a response to the smell of the rooting material regardless of the underlying motivation (play, comfort or other motivation), which is worth further investigation in future studies.

Wolves (Ryon et al., 1986) as well as wild (Mitchell and Kelly, 1992) and domestic dog breeds (Hepper and Wells, 2017; Frenkel and Parker, 1996; Frenkel et al., 2003) display rubbing and rolling behaviour when exposed to certain odours. In the wolf, the behaviour is thought to be carrying information about the prey back to the pack (Handelman, 2012), whereas in the African wild dog, rolling in a scent has been recorded in relation to scent marking (Parker, 2010). While examples of scent-marking are abundant, only few studies have shown rubbing or rolling as a response to an odour of non-social origin, and the majority of these are examples from carnivores (Gosling and McKay, 1990). In domestic dogs, this behaviour is widely known as rolling in malodourous scents (at least to the human nose) (Hepper and Wells, 2017). Although this behaviour is common, and often well-known by dog owners, the underlying reason for the behaviour is not fully understood (Hepper and Wells, 2017; Gosling and McKay, 1990). In scientific studies, the behaviour is most often mentioned as a risk behaviour spreading toxoplasma from dogs to their owners (Frenkel and Parker, 1996; Frenkel et al., 2003), but the behaviour does not appear to have been systematically described or analysed in domestic dogs. There are, nevertheless, several hypotheses on what function this behaviour may have for the animal: a mean to establish social attractiveness (Reiger, 1979; Ryon et al., 1986; Drea et al., 2002) or dominance (Gosling and McKay, 1990), indirect (low-risk) intraspecies communication (Gosling and McKay, 1990), a way of carrying information back to the pack (Mertl-Millhollen et al., 1986; Drea et al., 2002), as camouflage (for predators) (Reiger, 1979; Ryon et al., 1986), means to deter predators (Allen et al., 2017) or insects (Weldon et al., 2003), a form of reinforcement or pleasure

(Horowitz, 2017), a way to alleviate skin infections (Rodriguez and Wrangham, 1993), learning about odours (Hepper and Wells, 2017), a way for collecting pungent odours similar to human perfume (Ryon et al., 1986; Fox, 2007) or self-anointing (Laska et al., 2007), or perhaps a behaviour retained in the genes which no longer serves a purpose for the domestic species (Hepper and Wells, 2017; Gosling and McKay, 1990). Like other mammals, pigs may be motivated to rub against and roll in odours of interest to them. In the current study, pigs were unable to physically reach the odour, hence rubbing and rolling in the odour per se was not possible, but the behaviours were still displayed by some of the pigs. A post hoc analysis indicated a potential correlation between expression of agonistic behaviour (pushing, displacement, and biting) and rubbing behaviour (post hoc Spearman correlation: $r^2 = 0.13$, $P < 0.001$), suggesting that pigs expressing rubbing behaviour showed signs of guarding access to the odour (for further results on agonistic behaviour see: Rørvang et al., 2023). Future studies should investigate if the motivation to rub and roll changes when the pig has physical access to the odour, over time, or if the social environment changes. To the best of our knowledge there is only one study investigating the effects of applying an odour to the pelt of the animal. Drea et al. (2002) applied carrion and camphor to the fur of captive spotted hyenas, and found that individuals covered in carrion received increased social interest by the pack, whereas the normal social greeting was disrupted when camphor wearing individuals were reunited with their pack. Hence, different olfactory stimuli seem to elicit different responses in the animals, which is in accordance with these results and other results in carnivores (Drea et al., 2002; Gosling and McKay, 1990; Gatti et al., 2021). The variation in responses elicited by different odours, could be due to the origin of the odours, the composition or complexity of the odour, any association the animal might have to the odours (e.g., apple might be associated with feeding), or the potency of the odour. None of the odours used in the current study were diluted, in an attempt to ensure each odour being equally potent, but it is possible, even likely, that odours differed in how strong or potent each pig perceived them. This may have affected the degree of attention given to each odour (Rørvang et al., 2023). Future studies should focus on testing dilution potencies, or gradient dilutions of individual odours to determine the detection points specifically for pigs (Søndergaard et al., 2010). It would also be interesting to use motivational tests to investigate how much pigs are willing to work for access to odours, if motivation differs between specific odours, and what behaviour they display upon gaining access.

In the previously mentioned Stolba and Woodgush (1989) study, rubbing behaviour was seen after sniffing and consisted of pigs rubbing the occipital region of their heads against the trunk of the trees (seen in adult and sub-adult animals). The authors suggested that this could be a marking behaviour, as it shares resemblance with several other species displaying head/neck rubbing or body rubbing as scent marking (e.g. rabbits: Hudson and Vodermayer, 1992, stoats: Murphy et al., 2022, coyotes: Barrette and Messier, 1980, bank voles: Rozenfeld and Rasmont, 1991, African civet: Ewe and Wemmer, 1974). Pigs may prefer rubbing against trees due to the roughness of the tree bark, however, the observations in the present study raise the possibility that the choice may be selected in part based on odour. Additionally, rubbing and rolling behaviour was predominantly displayed when pigs were exposed to odours from essential oils, and never after sniffing the odourless control samples. Essential oils are odorants derived from natural plant materials, and in the present study, pine was among the odours eliciting the most rubbing and rolling behaviour. Pigs have been observed rubbing against pine trees previously, which has been suggested as a means to repel lice and ticks due to pine resin (Dickson et al., 2001). Rubbing and rolling behaviour may potentially be a way to apply a specific odour to the body, and the behaviour may serve more than one function as a masking or signalling behaviour and as skin care. The study of behavioural responses of pigs to odours has only just started, and many of the aspects raised here warrant further investigation.

5. Conclusion

We found that, when exposed to odours, pigs display rubbing and rolling behaviour even though pigs had no physical access to rub or roll in the odours. Overall, essential oils (lavender, thyme, blood orange, aniseed, cedarwood, cinnamon bark, ginger, and pine) elicited more of the behaviours than the synthetic perfumes (vanilla, musk, apple, and jasmine) or the odourless control. All odours elicited rubbing whereas only four odours (blood orange, ginger, lavender, and pine) elicited rolling. Scent-rubbing/scent rolling is a well-known behaviour in zoo carnivores and pets, although the function is not clear. This is the first report of rubbing and rolling as a response to odour exposure in pigs. The motivation for performing these behaviours is unknown but may include skin care, comfort behaviour or marking behaviour. Further studies allowing pigs physical access to rub and roll in different odours may elucidate the underlying motivation.

Funding

The study was connected to a larger project funded by The Swedish Research Council Formas, Sweden, grant number: 2020-01286, led by the lead author MVR. The contribution of Dr Sarah-Lina Aagaard Schild was funded by the Innovation Centre for Organic Farming, Aarhus N, Denmark. These funders had no role in the design of the experiment, the curating of data, the analyses, the interpretation of result or the writing of the manuscript.

CRediT authorship contribution statement

Author contributions according to CRediT in the order authors appear on the paper. **MVR:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Supervision, and Project administration. **SLS:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, and Funding acquisition. **AW:** Conceptualisztion, Methodology, Writing – original draft, Writing – review & editing, and Supervision. **JS:** Methodology, Investigation, Writing – original draft, and Writing – review & editing. **AV:** Conceptualization, Methodology, and Writing – review & editing. **RG:** Investigation, and Writing – review & editing. **BLN:** Conceptualization, Methodology, and Writing – review & editing, and Supervision. All co-authors have read and approved the version of the manuscript that is submitted

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: SLAS is employed by the Innovation Centre for Organic Farming, Denmark. The company is a non-political institution and thus the political interest of its owner organisations are not influencing the decision-making or scientific work of the company. All other authors declare no conflict of interest.

Data availability

All data supporting the conclusions in the article are publicly available via SND.se, using the DOI: http://doi.org/10.5878/kc64-wd49.

Acknowledgements

The authors would like to thank The Swedish Research Council Formas, Sweden, for funding the project. Secondly, we would like to thank all pigs involved, and the Research Center Lövsta, Uppsala, Sweden, for great collaboration and participation. We would also like to thank Moses Gadri for his assistance during the experiments, and Innovation Centre for Organic Farming, Aarhus N, Denmark, for funding the contribution of Dr Sarah-Lina Aagaard Schild. Lastly, we would like to express our gratitude to Dr Jen-Yun Chou, Teagasc, Ireland, and Dr Céline Tallet and Dr Caroline Clouard, INRAE, France, for discussions on pig olfaction.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2023.106022.

References

Allen, M.L., Gunther, M.S., Wilmers, C.C., 2017. The scent of your enemy is my friend? The acquisition of large carnivore scent by a smaller carnivore. J. Ethol. 35 (1), 13–19. https://doi.org/10.1007/s10164-016-0492-6.

Barrette, C., Messier, F., 1980. Scent-marking in free-ranging coyotes, Canis latrans. Anim. Behav. 28 (3), 814–819. https://doi.org/10.1016/S0003-3472(80)80141-2.

Bateson, M., P. Martin, 2021. Measuring Behaviour: an Introductory Guide. Cambridge University Press. ⟨https://doi.org/10.1017/9781108776462⟩.

Bolhuis, J.E., Schouten, W.G.P., Schrama, J.W., Wiegant, V.M., 2005. Behavioural development of pigs with different coping characteristics in barren and substrate-enriched housing conditions. Appl. Anim. Behav. Sci. 93 (1–4), 213–228. https://doi.org/10.1016/j.applanim.2005.01.006.

Bolhuis, J.E., Schouten, W.G.P., Schrama, J.W., Wiegant, V.M., 2006. Effects of rearing and housing environment on behaviour and performance of pigs with different coping characteristics. Appl. Anim. Behav. Sci. 101 (1–2), 68–85. https://doi.org/10.1016/j.applanim.2006.01.001.

Bracke, M.B.M., 2011. Review of wallowing in pigs: description of the behaviour and its motivational basis. Appl. Anim. Behav. Sci. 132 (1–2), 1–13. https://doi.org/10.1016/j.applanim.2011.01.002.

Day, J.E.L., Kyriazakis, I., Lawrence, A.B., 1995. The effect of food-deprivation on the expression of foraging and exploratory-behavior in the growing pig. Appl. Anim. Behav. Sci. 42 (3), 193–206. https://doi.org/10.1016/0168-1591(95)93889-9.

Dickson, J.G., Mayer, J.J., Dickson, J.D., 2001. Wild hogs. In: Dickson, J.G. (Ed.), Wildlife of Southern Forests: Habitat and Management. Hancock House Publishers, pp. 191–208.

Drea, C.M., Vignieri, S.N., Cunningham, S.B., Glickman, S.E., 2002. Responses to olfactory stimuli in spotted hyenas (Crocuta crocuta): I. Investigation of environmental odors and the function of rolling. J. Comp. Psychol. 116 (4), 331–341. https://doi.org/10.1037/0735-7036.116.4.331.

Ewe, R.F., Wemmer, C., 1974. The behaviour in captivity of the African civet. Civettictus Civetta (Schreber). Z. für Tierpsychol. 34 (4), 359–394. https://doi.org/10.1111/j.1439-0310.1974.tb01809.x.

Fox, M., 2007. Dog Body, Dog Mind: Exploring Canine Consciousness and Total Well-being. Rowman & Littlefield, Lanham (USA).

Fraser, A.F., 1970. Studies on heat stress in pigs in a tropical environment. Trop. Anim. Health Prod. 2, 76–86. https://doi.org/10.1007/BF02359573.

Frenkel, J.K., Lindsay, D.S., Parker, B.B., Dobesh, M., 2003. Dogs as possible mechanical carriers of Toxoplasma, and their fur as a source of infection of young children. Int. J. Infect. Dis. 7 (4), 292–293. https://doi.org/10.1016/s1201-9712(03)90112-3.

Frenkel, J.K., Parker, B.B., 1996. An apparent role of dogs in the transmission of Toxoplasma gondii: the probable importance of xenosmophilia. Ann. N. Y. Acad. Sci. 791 (1), 402–407. https://doi.org/10.1111/j.1749-6632.1996.tb53546.x.

Gatti, R.C., Velichevskaya, A., Gottesman, B., Davis, K., 2021. Grey wolf may show signs of self-awareness with the sniff test of self-recognition. Ethol. Ecol. Evol. 33 (4), 444–467. https://doi.org/10.1080/03949370.2020.1846628.

Gosling, L.M., McKay, H.V., 1990. Scent-rubbing and status signalling by male mammals. Chemoecology 1, 92–95. https://doi.org/10.1007/BF01241649.

Guiraudie-Capraz, G., Slomianny, M.-C., Pageat, P., Malosse, C., Cain, A.-H., Orgeur, P., Meillour, P.N.-L., 2005. Biochemical and chemical supports for a transnatal olfactory continuity through sow maternal fluids. Chem. Senses 30 (3), 241–251. https://doi.org/10.1093/chemse/bji020.

Hafez, E.S.E., L.J. Sumption, J.S. Jakway. 1962. The behaviour of swine. In: Hafez, E.S. E., The Behaviour of Domestic Animals, Tindall and Cox, London 334–369.

Handelman, B. 2012. Canine Behavior: a Photo Illustrated Handbook, Dogwise Publishing, ISBN: 9780976511892.

Hepper, P.G., Wells, D.L., 2017. Olfactory behaviour in companion animals. In: Nielsen, B.L. (Ed.), Olfaction in Animal Behaviour and Welfare. CABI International, pp. 201–213. https://doi.org/10.1079/9781786391599.0201.

Horowitz, A. 2017. “Smeller.” Chapter 2 In: “Being a Dog: following the Dog Into A World of Smell, ISBN: 9781476796024, Scribner, New York, 7–31.

Hothersall, B., Harris, P., Sörtoft, L., Nicol, C.J., 2010. Discrimination between conspecific odour samples in the horse (Equus caballus). Appl. Anim. Behav. Sci. 126 (1–2), 37–44. https://doi.org/10.1016/j.applanim.2010.05.002.

Hudson, R., Vodermayer, T., 1992. Spontaneous and odour-induced chin marking in domestic female rabbits. Anim. Behav. 43 (2), 329–336. https://doi.org/10.1016/S0003-3472(05)80228-3.

Huynh, T.T.T., Aarnink, A.A., Gerrits, W.J.J., Heetkamp, M.J.H., Canh, T.T., Spoolder, H. A.M., Kemp, B., Verstegen, M.W.A., 2005. Thermal behaviour of growing pigs in response to high temperature and humidity. Appl. Anim. Behav. Sci. 91 (1–2), 1–16. https://doi.org/10.1016/j.applanim.2004.10.020.

Ingram, D.L., 1965. Evaporative cooling in the pig. Nature 207 (995), 415–416. https://doi.org/10.1038/207415a0.

Jakobsen, M. , 2018. Integrating Foraging and Agroforestry Into Organic Pig Production - Environmental and Animal Benefits. Ph.D., Agroecology, Aarhus University. ⟨https://pure.au.dk/portal/en/publications/integrating-foraging-and-agroforestry-into-organic-pig-production–environmental-and-animal-benefits(4e90034a-143e-473c-a8ea-e34442e8826e).html⟩.

Jones, J.B., Wathes, C.M., Persaud, K.C., White, R.P., Jones, R.B., 2001. Acute and chronic exposure to ammonia and olfactory acuity for n-butanol in the pig. Appl. Anim. Behav. Sci. 71 (1), 13–28. https://doi.org/10.1016/s0168-1591(00)00168-4.

Kilkenny, C., Browne, W.J., Cuthill, I.C., Emerson, M., Altman, D.G., 2010. Improving bioscience research reporting: the ARRIVE guidelines for reporting animal research. PLoS Biol. 8 (6) https://doi.org/10.1371/journal.pbio.3000410.

Kristensen, H.H., Jones, R.B., Schofield, C., White, R.P., Wathes, C.M., 2001. The use of olfactory and other cues for social recognition by juvenile pigs. Appl. Anim. Behav. Sci. 72 (4), 321–333. https://doi.org/10.1016/S0168-1591(00)00209-4.

Laska, M., Bauer, V., Salazar, L.T.H., 2007. Self-anointing behavior in free-ranging spider monkeys (Ateles geoffroyi) in Mexico. Primates 48, 160–163. https://doi.org/10.1007/s10329-006-0019-9.

Lee, A.C.Y., Schantz, P.M., Kazacos, K.R., Montgomery, S.P., Bowman, D.D., 2010. Epidemiologic and zoonotic aspects of ascarid infections in dogs and cats. Trends Parasitol. 26 (4), 155–161. https://doi.org/10.1016/j.pt.2010.01.002.

McGlone, J.J., Devaraj, S., Garcia, A., 2019a. A novel boar pheromone mixture induces sow estrus behaviors and reproductive success. Appl. Anim. Behav. Sci. 219, 104832 https://doi.org/10.1016/j.appanim.2019.104832.

McGlone, J., Garcia, A., Rakhshandeh, A., 2019b. Multi-farm analyses indicate a novel pheromone improves sow reproductive performance. Animals 9, 37–47. https://doi.org/10.3390/ani9020037.

McMillan, B.R., Cottam, M.R., Kaufman, D.W., 2000. Wallowing behavior of American bison (Bos bison) in tallgrass prairie: an examination of alternate explanations. Am. Midl. Nat. 144 (1), 159–167. ⟨https://www.jstor.org/stable/3083019⟩.

Mendl, M., Randle, K., Pope, S., 2002. Young female pigs can discriminate individual differences in odours from conspecific urine. Anim. Behav. 64, 97–101. https://doi.org/10.1006/anbe.2002.3040.

Mertl-Millhollen, A.S., Goodmann, P.A., Klinghammer, E., 1986. Wolf scent marking with raised- leg urination. Zoo. Biol. 5 (1), 7–20. https://doi.org/10.1002/zoo.1430050103.

Mitchell, J., Kelly, A., 1992. Evaluating odour attractants for control of wild dogs. Wildl. Res. 19 (2), 211–219. https://doi.org/10.1071/WR9920211.

Morrow-Tesch, J., McGlone, J.J., 1990a. Sensory systems and nipple attachment behavior in neonatal pigs. Physiol. Behav. 47 (1), 1–4. https://doi.org/10.1016/0031-9384(90)90034-2.

Morrow-Tesch, J., McGlone, J.J., 1990b. Sources of maternal odors and the development of odor preferences in baby pigs. J. Anim. Sci. 68 (11), 3563–3571. https://doi.org/10.2527/1990.68113563x.

Murphy, E.C., Sjoberg, T., Agnew, T., Sutherland, M., Andrews, G., Williams, R., Williams, J., Ross, J., Clapperton, B.K., 2022. Body odours as lures for stoats mustela erminea: captive and field trials. Animals 12 (3), 394.8. https://doi.org/10.3390/ani12030394.

Nowicki, J., Swierkosz, S., Tuz, R., Schwarz, T., 2015. The influence of aromatized environmental enrichment objects with changeable aromas on the behaviour of weaned piglets. Vet. Arh. 85 (4), 425–435.

Ocepek, M., Newberry, R.C., Anderson, I.L., 2020. Which types of rooting material give weaner pigs most pleasure? Appl. Anim. Behav. Sci. 231, 105070 https://doi.org/10.1016/j.applanim.2020.105070.

Ogle, D.H., J.C. Doll, A.P. Wheeler, A. Dinno, 2023. FSA: simple fisheries stock assessment methods. R-program. R Package Version 0.9.4. ⟨https://fishr-core-team.github.io/FSA/⟩.

Oostindjer, M., Bolhuis, J.E., Simon, K., van den Brand, H., Kemp, B., 2011. Perinatal flavour learning and adaptation to being weaned: all the pig needs is smell. PLoS One 6 (10). https://doi.org/10.1371/journal.pone.0025318.

Parker, M. , 2010. Territoriality and Scent Marking Behavior of African Wild Dogs in Northern Botswana (Ph.D. thesis). University of Montana. ⟨https://scholarworks.umt.edu/etd/954/⟩.

Pond, W.G., K.A. Houpt., 1978. The Biology of The Pig, first ed., Cornell University.

R-Core-Team., 2022. R: a Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria.

Reiger, I., 1979. Scent rubbing in carnivores. Carnivore 2 (1), 17–25.

Rekwot, P.I., Ogwu, D., Oyedipe, E.O., Sekoni, V.O., 2001. The role of pheromones and biostimulation in animal reproduction. Anim. Reprod. Sci. 65 (3–4), 157–170. https://doi.org/10.1016/s0378-4320(00)00223-2.

Rodriguez, E., Wrangham, R., 1993. Zoopharmacognosy: the use of medicinal plants by animals. In: Downum, K.R., Romeo, J.T., Stafford, H.A. (Eds.), Phytochemical Potential of Tropical Plants. Plenum Press, New York. https://doi.org/10.1007/978-1-4899-1783-6_4.

Rørvang, M.V., Aa. Schild, S.-L., Stenfelt, J., Grut, R., Gadri, M.A., Valros, A., Nielsen, B. L., Wallenbeck, A., 2023. Odor exploration behavior of the domestic pig (Sus scrofa) as indicator of enriching properties of odors. Front. Behav. Neurosci. 17 https://doi.org/10.3389/fnbeh.2023.1173298.

Rørvang, M.V., Jensen, M.B., Nielsen, B.L., 2017. Development of test for determining olfactory investigation of complex odours in cattle. Appl. Anim. Behav. Sci. 196, 84–90. https://doi.org/10.1016/j.applanim.2017.07.008.

Rozenfeld, F.M., Rasmont, R., 1991. Odour cue recognition by dominant male bank voles, Clethrionomys glareolus. Anim. Behav. 41 (5), 839–850. https://doi.org/10.1016/S0003-3472(05)80351-3.

R-studio Team, 2022. R-Studio: Integrated Development for R, R-Studio, PBC, Boston, MA.

Ryon, J., Fentress, J.C., Harrington, F.H., Bragdon, S., 1986. Scent rubbing in wolves (Canis lupus): the effect of novelty. Can. J. Zool. 64 (3), 573–577. https://doi.org/10.1139/z86-084.

Schild, S-L.Aa., Rørvang, M.V., 2023. Pig olfaction: the potential impact and use of odors in commercial pig husbandry. Front. Anim. Sci., Sec. Animal Welfare and Policy. 4 https://doi.org/10.3389/fanim.2023.1215206.

Sherwin, C.M., Christiansen, S.B., Duncan, I.J., Erhard, H.W., Lay Jr, D.C., Mench, J.A., O'connor, C.E., Petherick, J.C., 2003. Guidelines for the ethical use of animals in applied ethology studies. Appl. Anim. Behav. Sci. 81 (3), 291–305. https://doi.org/10.1016/S0168-1591(02)00288-5.

Søndergaard, L.V., Holm, I.E., Herskin, M.S., Dagnæs-Hansen, F., Johansen, M.G., Jørgensen, A.L., Ladewig, J., 2010. Determination of odor detection threshold in the Göttingen minipig. Chem. Senses 35 (8), 727–734. https://doi.org/10.1093/chemse/bjq076.

Stolba, A., Woodgush, D.G.M., 1989. The behavior of pigs in a semi-natural environment. Anim. Prod. 48, 419–425. https://doi.org/10.1017/S0003356100040411.

Studnitz, M., Jensen, M.B., Pedersen, L.J., 2007. Why do pigs root and in what will they root? A review on the exploratory behaviour of pigs in relation to environmental enrichment. Appl. Anim. Behav. Sci. 107 (3–4), 183–197. https://doi.org/10.1016/j.applanim.2006.11.013.

Sundberg, H., Døving, K., Novikov, S., Ursin, H., 1982. A method for studying responses and habituation to odors in rats. Behav. Neural Biol. 34 (1), 113–119. https://doi.org/10.1016/S0163-1047(82)91501-1.

The Swedish Livestock Research Centre, 2017. Resources at the Swedish Livestock Research Centre.The Swedish Livestock Research Centre, Faculty of Veterinary Medicine and Animal Science, The Swedish University of Agricultural Sciences. 〈https://www.slu.se/globalassets/ew/org/andra-enh/vh/lovsta/dokument/resources-at-slu-lovsta-march-2017-webb.pdf〉. (Accessed 12 February 2023).

Van de Weerd, H.A., Docking, C.M., Day, J.E.L., Avery, P.J., Edwards, S.A., 2003. A systematic approach towards developing environmental enrichment for pigs. Appl. Anim. Behav. Sci. 84 (2), 101–118. https://doi.org/10.1016/S0168-1591(03)00150-3.

Weldon, P.J., Aldrich, J.R., Klun, J.A., Oliver, J.E., Debboun, M., 2003. Benzoquinones from millipedes deter mosquitoes and elicit self-anointing in capuchin monkeys (Cebus spp.). Naturwissenschaften 90 (7), 301–304. https://doi.org/10.1007/s00114-003-0427-2.

White, E.B. , 1952. Charlotte's Web, Harper and Brothers.

Wickham, H. , 2009. ggplot2. P-package, first ed., Use R! New York, Springer.

Wood-Gush, D.G.M., Vestergaard, K., 1989. Exploratory behavior and the welfare of intensively kept animals. J. Agric. Ethics 2 (2), 161–169. https://doi.org/10.1007/BF01826929.

Yang, M., Crawley, J.N., 2009. Simple behavioral assessment of mouse olfaction. Curr. Protoc. Neurosci. Chapter 8: Unit. 8, 24. https://doi.org/10.1002/0471142301.ns0824s48.