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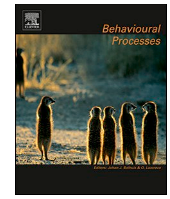

Executing specific foraging behaviours does not represent a general goal state of foraging in dry sows (*Sus scrofa*)

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ABSTRACT

Intensively housed domestic pigs (*Sus scrofa*) have little opportunity to perform diverse foraging behaviour though they still seem strongly motivated to do so. Here, we investigated whether the execution of specific behaviours may in itself satisfy their foraging motivation.

We elicited the specific foraging behaviours rooting, grazing, and biting & chewing by providing 24 dry sows with three different substrates. Sows visited three pens consecutively. Two of the three substrates were offered one in pen 1 and the other in pen 2, whereas pen 3 provided the three substrates simultaneously. In the control condition, all three materials were provided in all pens.

In pen 1 and 2, the sows predominantly showed those foraging behaviours that were to be elicited by the specific substrates. Sows spent less time in pens with a single substrate compared with when all substrates were available. Moreover, durations of the specific behaviours which had not been performed in pen 1 and 2 increased in pen 3. Finally, the lowest proportion of time was spent in pen 3 in the control condition.

In conclusion, the results indicate that performing single behaviours of the foraging repertoire did not satisfy the sows' overall foraging motivation.

1. Introduction

The proximate goal of a behaviour may often not coincide with the behaviour's function (Tinbergen, 1963). The function of behaviours often seems obvious; e.g. foraging serves to provide energy to an organism. The proximate goal of foraging, however, is less clear. What is the external event or internal state, which an animal needs to reach such that the control mechanism (in the brain) lowers or even disengages the foraging motivation? Foraging in domestic pigs (*Sus scrofa*) is a likely example where the function of the behaviour does not serve as its main goal. In modern production systems, feed for pigs consists usually of mixtures that fulfil effectively the function of satiety. Nevertheless, the motivation to forage seems to remain strong even in ad libitum fed growing pigs (Day et al., 1995) and dry sows in an experimental setting (Durrell et al., 1997). The goal state reflects how an animal perceives and deals with its environment and is therefore fundamental in understanding behaviour. Knowing about the specific goal state may be specifically important in respect to the welfare of animals in human care because the functionality of a behaviour is often provided by the housing conditions without the animals' need to reach the corresponding goal state (Gygax, 2017; Gygax and Hillmann, 2018). In respect to foraging in pigs, they may start to perform foraging behaviours on other substrates if the goal state of foraging cannot be reached. This may lead to stereotypic (e.g. bar biting, tongue flicking, and vacuum chewing; Arellano et al., 1992; Terlouw et al., 1991; Terlouw and Lawrence, 1993) or re-directed (biting ears and tails of other pigs; Day et al., 1995; Van De Weerd et al., 2005) oral behaviour. Given the difference between function and the goal state, animals may often not be able to perceive that the function in itself is achieved. This is why it is important to understand which goal state an animal seeks. In respect to pig foraging, it can therefore be concluded that foraging behaviour does neither seem to be principally controlled by the act of feed intake nor by the internal state of satiety, though the performance of stereotypies is modulated by satiety (Bergeron et al., 2000). Reaching a goal state is often not directly reflected in (and observable by) overt behaviour. Therefore, no standard procedures for assessing goal states in animals exist and novel approaches to indirectly infer the reaching of goal states need to be developed.

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In semi-feral conditions, domestic pigs seem to have preserved the motivation to forage in a very similar way to wild boars. Under these circumstances, the domestic pigs' foraging consists of a variety of different behaviours (Stolba and Wood-Gush, 1989) that reflect the highly diversified feed spectrum. Pigs feed on above- and underground plant parts (e.g. grass, seeds, fruits, leafs, branches, roots) as well as small animals (e.g. insects, worms, snails; Briedermann, 2009; Porzig and Sambraus, 1991). Moreover, pigs spend a major part of their active time with foraging (> 50% in semi-feral conditions; Stolba and Wood-Gush, 1989). In intensively housed pigs, the short time needed for feeding concentrated feed and the absence of substrates allowing for a diversified foraging repertoire are likely to contribute to foraging motivation persisting even after feeding.

Foraging helps to locate feed and food feedback is certainly a strong (proximate) signal to regulate foraging motivation. Therefore, the behavioural context of foraging overlaps with the contexts of feeding but also with exploration. Day et al. (1995) found that rooting behaviour in growing pigs increased when they were fed restrictively. Haskell et al. (1996a) observed that food feedback could maintain, at least in the short run, sows' foraging behaviour. They concluded that the persistent oral behaviour is closely controlled by the details of a given foraging situation and therefore factors other than a 'controlled pre-programmed loop of feeding behaviour' (see also Haskell et al., 1996b). Similarly, Holm et al. (2008) reported that pigs preferred rooting material with food feedback over rooting material without feedback (see also Jensen et al., 2010). Moreover, Studnitz and Jensen (2002) found that an increasing duration of deprivation did not monotonously increase the motivation to root in gilts. In contrast, the results of Beattie and O'Connell (2002) indicated that rooting after food feedback seemed to stop only when pigs had learnt how much food will be available. In their experiment, pigs showed more rooting without a known quantity of food reward and showed more rooting with more highly restricted feed levels.

Exploration may also play a role in foraging. Day et al. (1995) found that growing pigs, regardless of their satiation level, increased the number of visits to a foraging area when novel objects were presented in comparison to the presentation of feed only and a control situation without feed. This aspect of the pigs' behaviour was not influenced by their satiety level. On the other hand, the presence of an object did not have an effect on the duration of rooting (see above). Studnitz et al. (2007) concluded that foraging behaviour was best maintained if exploration was possible at the same time.

Neither the research on food feedback nor exploration can explain how behaviours of the foraging repertoire can become rigid actions (redirected or stereotypic oral behaviour). Therefore, we raise the question what the proximate goal of foraging behaviour could be. Specifically, we investigated whether specific foraging behaviours can satisfy the overall motivation to forage and could, therefore, present in itself a proximate goal state of foraging (Jensen and Toates, 1993). We elicited specific foraging behaviours in response to different substrates and assessed the remaining foraging motivation. To do so, we offered dry sows these substrates in different sequences and for a maximum duration of 40 min each in the 1st and 2nd of three pens. In the 3rd pen, all three substrates were available to check for any remaining motivation. We chose sows for our experiment because they need less habituation in an experiment conducted with individually separated animals compared with growing pigs, though, as a production standard, these sows were restrictively fed to ensure ease of farrowing. Therefore, sows could have been slightly hungry during our experimental sessions (Day et al., 1995) depending on when they had their last meal. In addition, all substrates that we provided were likely to include some food feedback at a low frequency (Haskell et al., 1996a). Both these aspects might have increased the overall foraging motivation in the sows. Given these promotors of motivation in our experiment, a reduction in feeding motivation in response to performing specific foraging behaviours would be an even stronger support that the behaviours themselves serve as a goal state. We expected to see a clear reduction in the remaining foraging motivation, measured in the 3rd pen, after performing specific types of foraging behaviours in the 1st and 2nd pen if one (or several) of these foraging behaviours served as the goal state of foraging.

2. Materials and methods

2.1. Animals and housing

The study was conducted with 24 dry (pregnant but non-lactating) sows at the Agroscope research farm (Tänikon, Switzerland) between January and May 2017. All sows were of the breed Swiss Large White with birth years between 2012 and 2016. For a given sow, the last experimental session was at least two weeks before the calculated farrowing date.

The sows were run in a standard agricultural production cycle and housed in groups of up to 16 animals during the dry period. Their group housing pens consisted of an indoor area with straw bedding on concrete floor and a permanently accessible outdoor area with concrete floor. Straw was provided two times a week (about 0.5 kg per sow and week). The sows were fed restrictively with standard food mixture, receiving between 2.5 and 2.9 kg of feed per day (depending on their gestation state). They were fed individually at an electronic feeding station (automatic on-demand feeder), which allowed the sows to individually collect their feed, which they typically do in one single portion per day. A new feeding cycle starts at 3 a.m. and, usually, all sows had collected their feed before 9 a.m.. Additionally, they had access to hay (about 0.3 kg per sow and day) which was provided daily between 9 and 10 a.m. in racks mounted to the pens walls. As sows collected their feed from the feeding station at a similar time each day, as hay was provided daily at the same time, and as each sow was tested at a given time of day (see below), satiety was controlled for within sows.

Ethical approval for the study was obtained from the Veterinary Office of the Canton Thurgau (Switzerland; TG02/15, Approval No. 28629).

2.2. Procedure and experimental design

The 24 experimental sows were allocated to eight batches of three sows. Sows were tested individually and participated in eight different experimental sessions each. The eight sessions were conducted on eight different days. Usually, there were four test days in each of two weeks. Due to time constraints, three sows of one batch had three and five sessions in week 1 and 2, respectively. A session included the visits to three pens and lasted for a maximum of 40 min/pen (a total of 120 min). A given sow was always tested at the same time of day (at approximately 08:00, 10:15, or 14:00).

During the test sessions, sows had access to different foraging substrates offered in three experimental pens to which they had access successively within a session. For a session, the sow was allowed to exit from the group pen into the barn corridor and herded into the first of the experimental pens, which were situated approximately 10 m from the group pens on the opposite side of the corridor. All sows were accustomed to being handled and herded from standard management procedures and let themselves be guided willingly. The three experimental pens adjacent to each other measured 4.0 x 2.5 m each and were connected with doors. Each pen was equipped with a drinker. In each experimental pen, the sows were provided with either one or three different substrates (Fig. 1) which were chosen to elicit specific foraging and feeding behaviours. We based our choices of substrates on studies on enrichment materials for pigs (Bracke et al., 2007; Studnitz et al., 2007; Jensen et al., 2008), and investigated their suitability during pilot-trials with four different sows (not included in the experiment).

Earth materials were provided for rooting. An area of 2 x 2.5 m and 5 cm deep was filled half with stones (rounded pebbles of 3–9 cm in

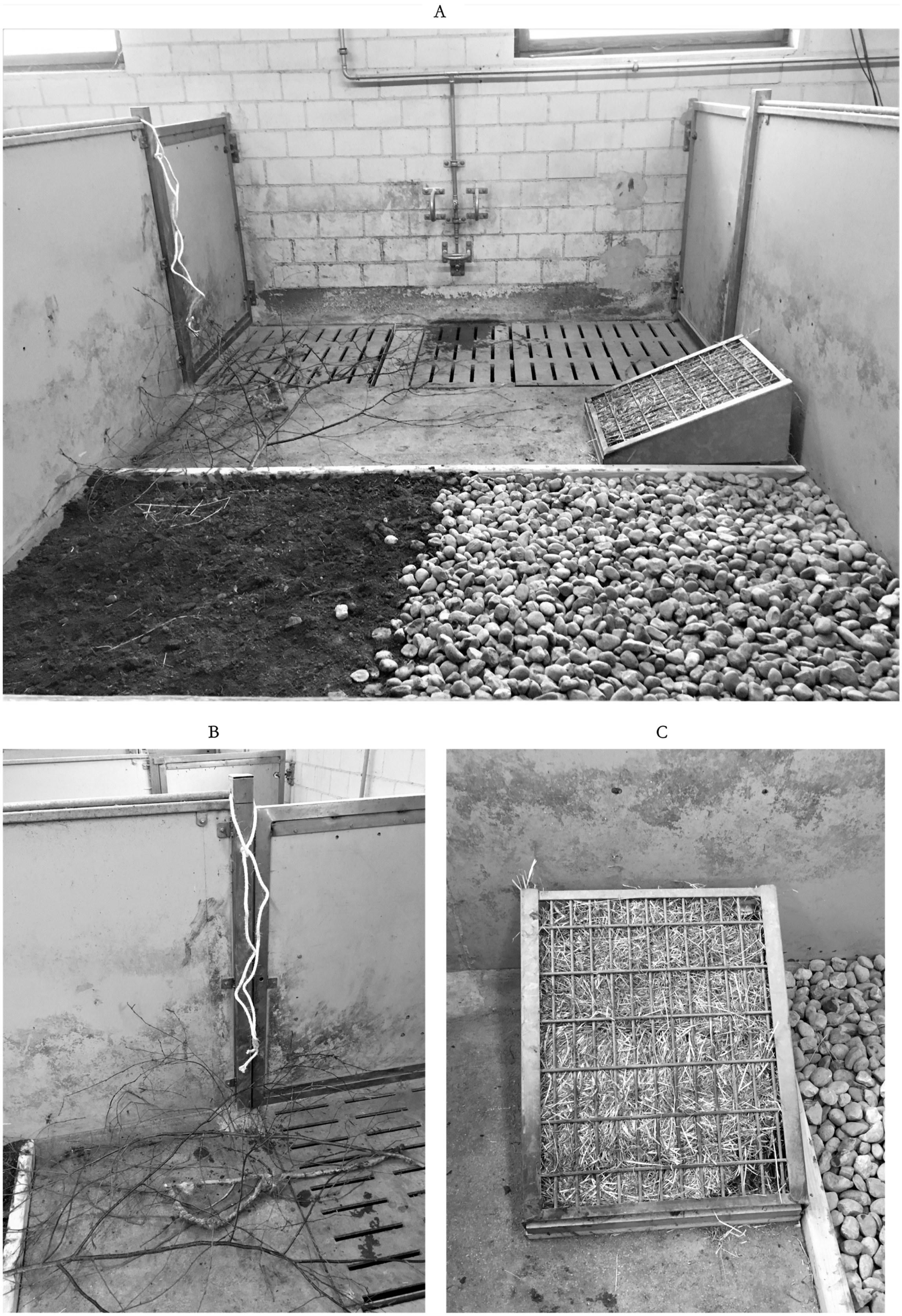

Fig. 1. Experimental pen with all three substrates provided; earth materials (A) in front, fibre materials (B) left rear, and grazer (C) right rear.

diameter) and half with common garden soil which also contained some smaller stones, dead plant parts, and small pieces of wood. If earth materials were not provided in a given pen they were covered with wooden boards.

A “grazer” was used to elicit grazing. The grazer consisted of a hay rack with a ground area of 64 x 54 cm and sloping side walls with a height of 34.5 cm at the highest and 8.5 cm at the lowest point. It was filled with non-chopped hay and grass silage which were accessible through a metal grid with a width of 6.5 x 4 cm (similar to a slow grazer™ for horses, www.grazingbox.com). The grazer was placed on the floor with the grid facing upwards. If the grazer was not provided in a given pen it was removed from the pen.

Fibre materials were provided for biting & chewing. A first sisal rope was placed on the floor and consisted of three ropes braided out to a tress of approximately 55 cm length. A second sisal rope was tied to the pen wall with two free ends of 1.25 m each. Additionally, two birch branches with a diameter of max. 3 cm and a length of 1–1.2 m (including all side branches) were placed on the floor. If the fibre materials were not provided in a given pen they were removed from the pen.

The substrates were replenished regularly. Soil was refreshed and stones were washed with water once a week. The sisal ropes were changed once in the middle of the experiment. Branches were renewed regularly when depleted or side branches had been chewed off. The grazer was refilled regularly to ensure that the sows could access the grass materials throughout their complete trials. The experimental pens were cleaned manually after each session from faeces and particles of the substrate when the latter were spread across the floor.

In the 1st and 2nd pen, only one of the three substrates was accessible for the sows in order to elicit specific foraging behaviours. In the 3rd pen, all three substrates were always available in order to test for remaining foraging motivation (Fig. 1). In the 1st and 2nd pen, different substrates were provided in each session. Based on the availability of the three substrates, there were six possible sequences for the first two pens; earth-fibre, fibre-earth, earth-grazer, grazer-earth, fibre-grazer, grazer-fibre. Each of these sequences was provided within one session for a given sow. Three of these possibilities were provided in experimental week 1, the other three in week 2. A fourth session was included each week. In this control session, all three experimental pens were equipped with all three substrates. It was expected that this would lead to a maximal reduction in foraging motivation in the 3rd pen. The sequences of the substrates between sessions were balanced across sows as well as possible given the number of sows. Each sow had a different sequence of sessions. Furthermore, a specific substrate combination within a session was applied only once on a given day. Due to an error in executing the experiment, one sow was tested twice with the substrate sequence fibre materials and grazer in pen 1 and 2, respectively, and did not receive the inverse sequence.

The amount of time granted to the sows in each pen was not an obvious choice. It should be sufficiently long in order to mimic the amount of time spent during a foraging bout under semi-feral conditions on the one hand but the motivation to forage should remain high on the other. As a seemingly sensible compromise, we allowed a duration of a maximum of 40 min in each pen before a sow was being led into the next pen or returned to the group after the 3rd pen. It is not currently clear whether this needs to be considered a long duration or only covering an initial foraging bout. To maintain a high level of foraging motivation, the maximum duration of 40 min per pen was terminated earlier if a sow did not interact anymore with the provided substrates for a continuous period of 5 min (performing other behaviour and/or manipulating pen equipment; Table 1). We considered such a break as a clear sign that the sow was no longer motivated to interact with any currently available substrate. In this case, the sow was either led into the next pen or returned to her group after the 3rd pen. The behaviour shown in these 5 min was omitted from analysis. Accordingly, performing other behaviour or manipulating pen equipment that occurred at the very end of the allocated time in a given pen (from minute 36 onwards) were omitted also from analyses because this behaviour could have led to a termination of the time in that pen.

2.3. Behavioural observations

The behaviour of the sows in the experimental pens was observed in real time via a video relay in order to not disturb the sows by the presence of the experimenter and to reduce experimenter influence as much as possible. A few sessions were scored based on the stored video relay after the sessions. According with our approach, the video quality was the same for all observations. For full surveillance, two cameras were installed in each pen (EverFocus EZ655, 8.5 mm (1/3“) SONY 960H WDR CCD, EverFocus Electronics GmbH, 46446 Emmerich am Rhein, Germany). The software ETHO (R. Weber, Agroscope, version 9.2.2) was used to continuously record the behaviours as defined in Table 1.

2.4. Data and statistical analyses

Data from pen 1 and 2 provided information on how successful the provided substrates were in eliciting specific behaviour. Data from pen 3 indicated the remaining motivation for foraging in dependence of the substrates available in pen 1 and 2.

Data handling and statistical analyses were conducted in R (version 3.5.1; R Core Team, 2018). We analysed the proportion of time spent in the pens (of the potential 40 min) and the total duration for which the different behaviours were performed in a pen (Table 1, 2) as outcome variables of linear mixed-effects models (lmer; package lme4; Bates et al., 2015). We used the logit transformation for the proportion of time and the log transformation for the durations. Therefore, we replaced the zeros in our data set by values that were 10% smaller than the smallest observed value larger than zero. This latter value can be considered as the detection level and zeros can be considered values below the detection level. If at all, this replacement made the values somewhat less extreme and in this sense it was a conservative procedure. If the proportion of time used was one, we proceeded in an analogous way: we replaced ones by maxObs + 0.1 · (1-maxObs), with maxObs being the maximum value observed that was smaller than one.

A preliminary analysis showed that the effect of the substrates on the behaviour in the 3rd pen did not seem to differ dependent on whether they were provided in the 1st or 2nd pen. The information on the exact sequence of the substrates was therefore omitted in our fixed effects. Our primary fixed effect was the type of substrate available in a given pen (conditions reflected by a factor with four levels: earth materials, grazer, fibre materials, and all). In pen 3, the same factor labels were defined but they indicated which of the substrates had been absent in pen 1 and 2. The second fixed effect was the pen number (factor with three levels. 1st, 2nd, 3rd pen). We also included the interaction between substrate and pen number as an additional fixed effect. The random effect contained experimental day, nested within week, nested within sow identity, nested within batch (to represent the hierarchical structure of the repeated measurements) and crossed with the calendar date of the session (to account for the fact that some sows were tested on the same day). We used sum-contrasts for our fixed factors to allow for interpreting main effects even in the presence of interactions in a full model. Accordingly, we always interpreted the full model (Forstmeier and Schielzeth, 2011). P-values for the fixed effects were calculated using a parametric bootstrap approach (PBmodcomp with 1000 samples; package pbkrtest; Halekoh and Højsgaard, 2014). We first compared the maximum model with a null model (including an intercept only). If this global test reached a low p-value, we further compared the maximum model with each of three models in which either the fixed effect of substrate, pen number, or the interaction was dropped. If not stated otherwise, the global as well as the more specific tests reached $p \leq 0.001$. Model assumptions were checked by graphical analysis of residuals (package Dharma; Hartig, 2018). These

Table 1
Ethogram of the recorded behaviours.

Behaviour	Definition
Rooting	The animal digs with a back-to-forth or sideways movement in materials using the snout for moving the material. The materials are moved by the nose of the animal for longer than 3 s and the movements can be accompanied by taking up materials in to the mouth.[a]
Manipulating stones	The animal manipulates stones with its mouth, teeth, and tongue or stones are sucked and/or chewed.
Grazing	The animal pulls out, bites off, and chews grass materials.
Biting & chewing	The animal manipulates the materials with the teeth. Materials are gnawed and/or bitten off or grinded.[b]
Pushing	The animal moves the materials with its nostral plate from one place to another.
Nosing	The animal moves its nostral plate across the surface of the materials in uninterrupted sweeping motions.
Manipulating pen equipment	The animal performs one of the behaviours listed above on pen equipment.
Other behaviour	The animal performs any other behaviour than those listed in the ethogram (i.e. resting).[d]
Drinking	The animal takes in water from the drinker.[c]
Pawing	The animal moves the material back-to-forth or sideways with a foot using either a fore or a hind leg. Occurred in 9 of 576 pen visits for a maximum duration of 0.98 min; no statistics conducted.
Carrying	The animal takes the materials up with its mouth and carries it from one place to another by taking at least three steps without manipulating the material. Occurred in 20 of 576 pen visits for a maximum duration of 5.01 min; no statistics conducted.

[a] Jensen et al. (2007).
[b] Elmore et al. (2012).
[c] Day et al. (1996).
[d] Tozawa et al. (2016).

assumptions may not have been fully met in some instances. This was likely due to the occurrence of zero values. Because the model estimates and confidence intervals looked reasonable given the data (Figs. 2,3), we were nevertheless satisfied with our models.

3. Results

In pen 1 and 2, the largest proportion of time was spent when all substrates were available (control), followed by the conditions with earth materials, grazer, and fibre materials (Fig. 2; if not stated otherwise, the global as well as the more specific tests all reached $p \leq 0.001$). In contrast, the largest proportion of time was spent in pen 3 when the sows did not have earth materials or the grazer available in pen 1 and 2. The smallest proportion of time was spent in pen 3 in the control condition, when all substrates had been available in pen 1 and 2 (Fig. 2).

In pen 1 and 2, earth materials elicited the specific behaviours rooting and manipulating stones, the grazer elicited grazing, and fibre materials elicited biting & chewing (Fig. 2). These behaviours were also shown in the control condition with all materials available. The behaviours that could not be shown before were shown longer in pen 3, i.e. more rooting and manipulating stones when earth materials had been absent, more grazing when the grazer had been absent, and more biting & chewing when fibre materials had been absent (Fig. 2). There were some cross-motivations in that rooting was also shown for somewhat longer when fibre materials had been absent, biting & chewing when earth materials had been absent, and manipulating stones when fibre materials had been absent (Fig. 2). Rooting generally increased from pen 1 to 3 as did manipulating stones on a lower absolute level.

Pushing was shown longer in pen 1 and 2 when earth materials, fibre materials, or all substrates were available and at a moderate duration in pen 3 in all conditions (Fig. 3). Nosing was shown in pen 1 and 2 with fibre materials and in the control condition and in pen 3, again, for a moderate duration in all conditions (Fig. 3; main effect pen: $p = 0.026$).

In pen 1 and 2, pen equipment was manipulated longer when earth materials and fibre materials, or all substrates were available. Manipulating pen equipment in pen 3 was shown slightly longer when no fibre materials had been available in pen 1 and 2 (Table, Fig. 3; main effect substrate: $p = 0.007$, interaction substrate x pen: $p = 0.16$). Other behaviour was shown for short durations in all pens. It was slightly longer in pen 1 and 2 when either earth materials or all substrates were available (Fig. 3; main effect pen: $p = 0.077$, interaction substrate x pen: $p = 0.011$).

Sows spent a low amount of time drinking independent of the experimental conditions (Fig. 3; global test: $p = 0.12$).

4. Discussion

We were successful in eliciting specific behaviours in pen 1 and 2. Earth materials triggered rooting and manipulating stones, sows were grazing on the grazer, and the fibre materials led to biting & chewing. If the execution of one or a few of these behaviours had served as the goal state of foraging, we would have expected that the motivation to continue with foraging behaviour was clearly reduced after executing these behaviours. This would then be detectable based on the behaviours performed in the 3rd pen, which was clearly not the case. No combinations of substrates in pen 1 and 2 could reduce the foraging motivation in a similar way as under the control condition when all materials were available in these pens. However, a specific motivation to show a specific behaviour in pen 3 was evident if the substrate eliciting this behaviour had not been available in pen 1 and 2; sows showed more rooting and manipulating stones when earth materials had been absent, more grazing when the grazer had been absent, or more biting & chewing when fibre materials had been absent. It can therefore be concluded that no single (or few) of the foraging behaviours served as a general goal state for all foraging behaviours. An alternative explanation could be that the different behaviours are independently motivated with each having its own specific goal state.

Based on the proportion of the available time spent in the different pens, the motivation to continue foraging in the 3rd pen was clearly lower in the control condition, when all substrates had already been available in the 1st and 2nd pen. The proportion of time spent foraging in the 3rd pen was larger if one of the substrates had been absent in the 1st and 2nd pen, indicating that the sows were still motivated to forage showing specifically the behaviour that had not been allowed in the first two pens. When only one of the substrates was available, the sows did not usually use up the full 40 min in the 1st and 2nd pen. In contrast, this was the case more often in the control conditions in pen 1 and 2 and in the 3rd pen. This may be a first indication that sows were motivated to show a variety of foraging behaviours. This view may be supported by the fact that manipulating pen equipment declined from the 1st to the 3rd pen; from pen to pen, additional substrates were provided on which sows could perform more variable behaviour. Given that pen equipment was manipulated most in the 1st pen and even when all substrates were available, sows may have been motivated for behaviours which they could not perform on any of the substrates in the current experiment.

Manipulating stones and pushing seemed to occur mainly in the 3rd pen, that is, towards the end of the possible foraging sequence. This

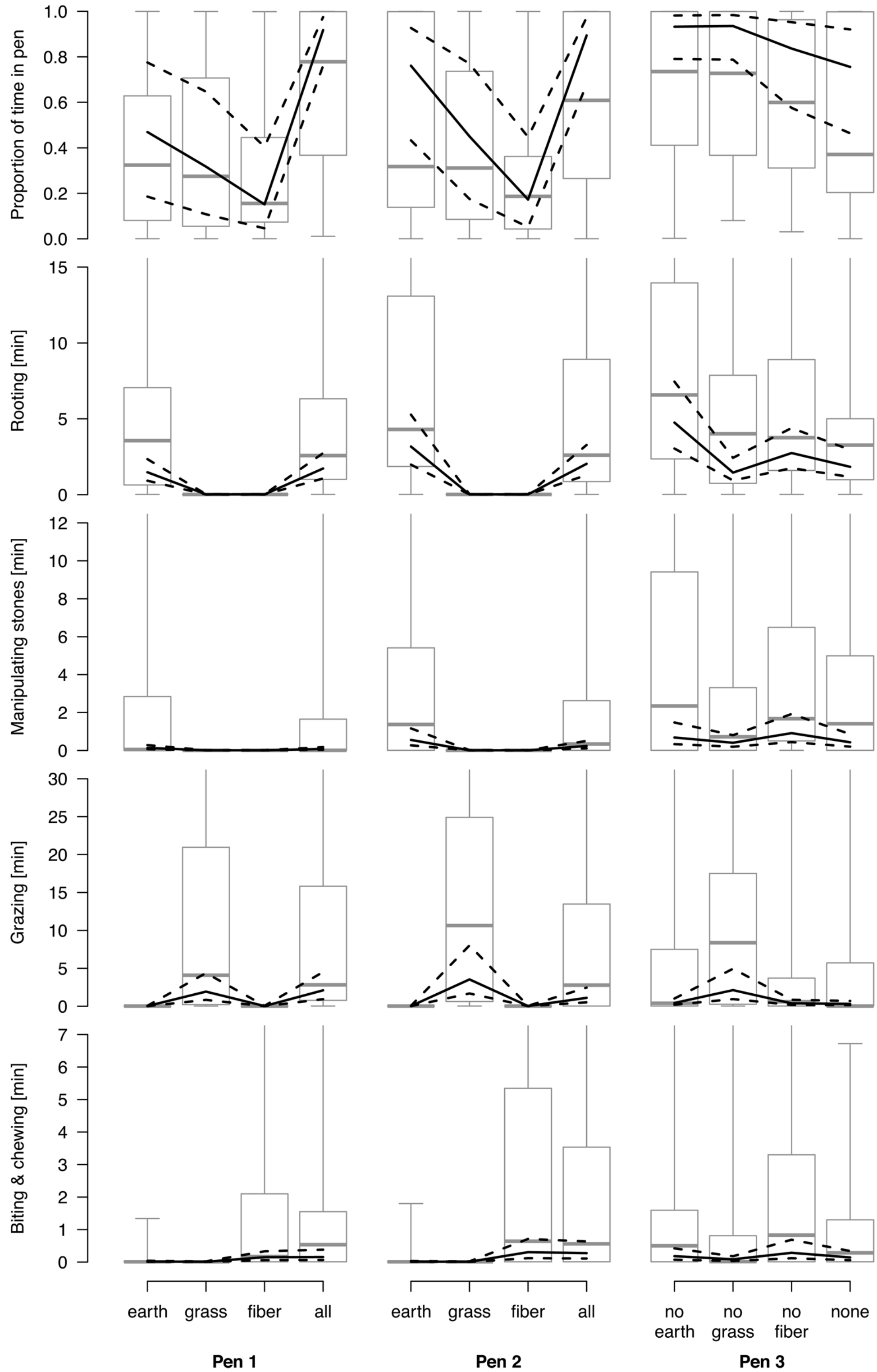

Fig. 2. from top to bottom: The proportion of time spent in each of the three pens as well as the duration spent with rooting, manipulating stones, grazing, and biting & chewing. For pen 1 and 2, the provided materials are indicated, whereas for pen 3 the material absent in pen 1 and 2 is indicated. Boxplots indicate data range, and the three quartiles. Thick lines indicate model estimates and dashed lines 95% confidence intervals.

could indicate an even more specific behavioural control in that sows may seek to perform these behaviours later during foraging. This may raise the more general question of whether sows were motivated to perform behaviours in a certain sequence. In order to disentangle the aspects of the variety of performed behaviour, specific sequences of performed behaviours, or specific goals for different foraging behaviours, further studies are needed that could be based on the experimental approach used here.

It has been suggested that foraging is closely linked to exploration in pigs (Day et al., 1995; Studnitz et al., 2007). In our experiment, substrates were provided that also allowed for some exploration that may have maintained the level of foraging motivation. Similarly, it had been found that food feedback seemed to be relevant in keeping up foraging motivations in pigs (Day et al., 1995; Haskell et al., 1996a, 1996b;

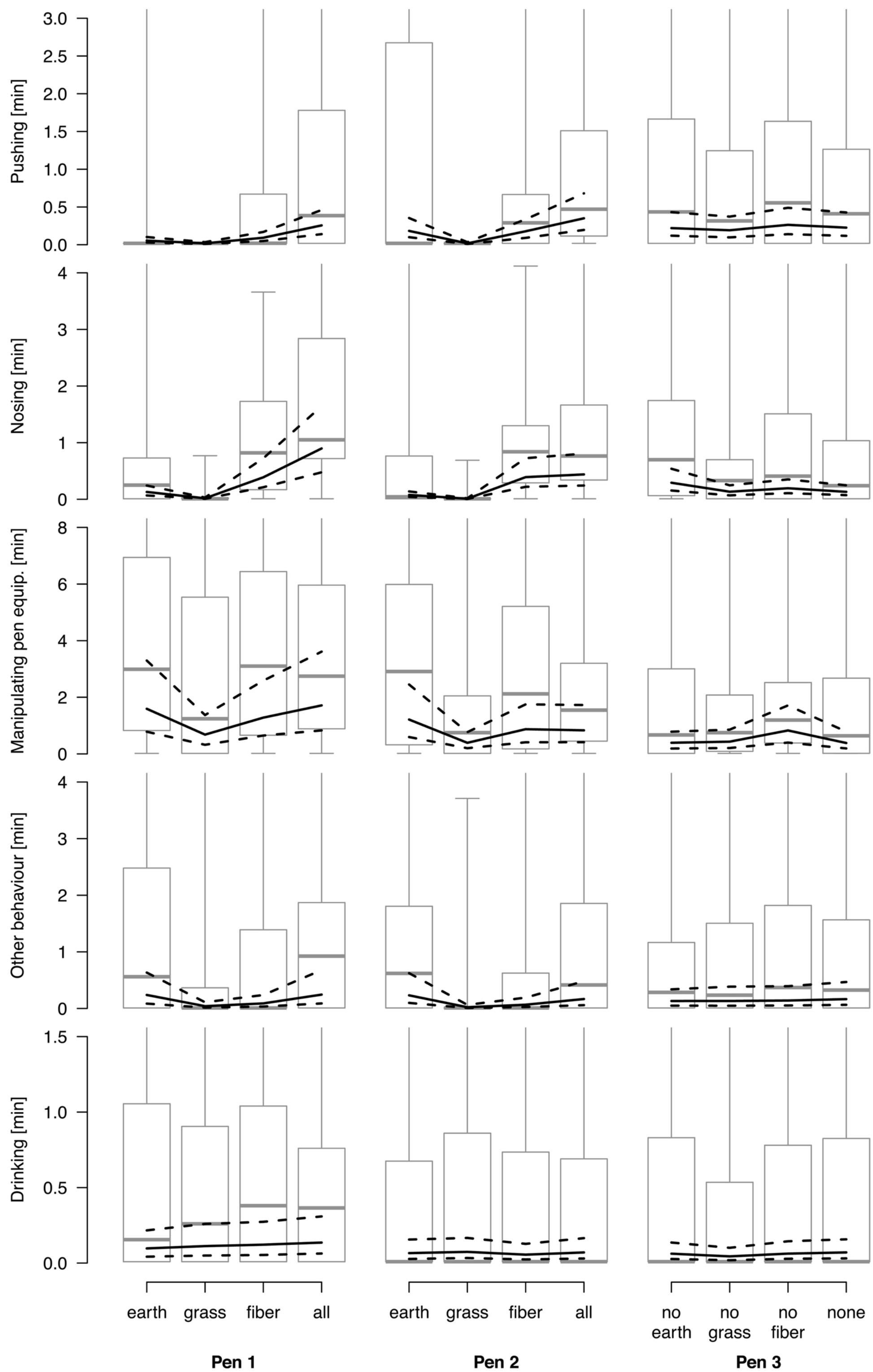

Fig. 3. from top to bottom: The duration spent with pushing, nosing, manipulating pen equipment, other behaviour, and drinking. For pen 1 and 2, the provided materials are indicated, whereas for pen 3 the material absent in pen 1 and 2 is indicated. Thick lines indicate model estimates and dashed lines 95% confidence intervals.

Holm et al., 2008; Jensen et al., 2010; Studnitz and Jensen, 2002). All materials here could provide some low but continuous levels of food feedback, which may have slightly decreased until next replenishment (but did not so in any striking way). Some edible parts were available in the earth materials, the grazer allowed to ingest grass materials but at a low frequency, and parts of the branches or some sisal fibres may also have been ingested. Therefore, it may not come as a surprise that the sows were motivated to keep foraging for up to 3 times 40 min in the control condition of this experiment. This would coincide with the observation that foraging motivation remains high if sows cannot learn the amount of food reward previously (Beattie and O'Connell, 2002). In our experiment, the sows did not know the amount of edible parts that they would be able to find. Our sows were fed restrictively as it is usual under farm conditions. This may have meant that some level of hunger could have helped to maintain foraging motivation. Therefore, a stronger effect in reduction of foraging motivation would possibly be observed in a replicate of our study carried out with pigs fed ad libitum. Similarly, the foraging control may be different with fattening pigs because they are younger and fed often ad libitum.

One of us (Gygax, 2017) has recently related proximate control to affective states in animals. Given that notion, we can speculate that sows do want to forage here but do not easily reach a state of liking what they achieve. If we follow these suggestions further and accept that liking induces a more profound positive state than wanting, the withholding of foraging opportunities in pigs may be highly detrimental to their emotional state and, therefore, to their welfare. This is even more so because a repeated mismatch between expectation (what goal state pigs want to reach) and outcome (failure to reach the foraging goals) is likely to lead to a more negative mood state which may result in a vicious circle through negative feedback. Given this speculation, it seems all the more important to understand what goal(s) pigs try to achieve while they are foraging.

We did not find that eliciting a specific behaviour based on a given substrate on its own clearly satisfies the general foraging motivation. Therefore, the specific behaviours do not seem to serve as goal states for foraging as a whole. For practical applications and with regard to animal welfare, this indicates that it is still the most recommendable option to provide dry sows with materials that are complex, changeable, destructible, manipulable, and contain some edible parts (Studnitz et al., 2007) if motivation to forage is to be reduced in pig husbandry.

Declaration of interest

None.

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