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A novel boar pheromone mixture induces sow estrus behaviors and reproductive success

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ABSTRACT

Androstenone is a molecule found in boar saliva and fat, which has been thought to be the male pig sexual pheromone. We previously identified and confirmed three boar-unique molecules in saliva, namely, quinoline (Q), androstenol (AL) and androstenone (AN). This study quantified the sexual behavioral responses of the molecules among post-weaning sows (days 4 and 5). Among 947 weaned sows, the percentage of sexual behaviors was increased by Boar Saliva Analog (BSA; a mixture of Q, AL and AN) relative to a vehicle control (isopropyl alcohol; ISO) or each molecule alone. A sexual behavior score was calculated for each molecule that combined standing still, pricked ears and vocalizations. BSA caused an increase in the standing reflex (standing still), pricked ears and vocalizations compared to ISO. BSA increased sexual behavior score by 63.9% over ISO while androstenone increased the sexual behavior score by only 13.5% over ISO. BSA was more effective than androstenone alone in the induction of sexual behaviors. It cuased more weaned sows to express behavioral estrus and to stand for insemination at a higher rate than boar exposure alone. Thus, the overt expression of sexual behaviors in weaned sows caused by BSA strongly suggests that the boar sexual pheromone is likely to be a mixture of three unique volatile molecules.

1. Introduction

Nearly 1 billion pigs on commercial farms in the world provide meat for much of the world. Pigs on modern, commercial farms are often bred by artificial insemination while a live adult boar stands nearby. The adult boar produces copious amounts of saliva when near a sow in estrus. Patterson (1968a,b) found 3α-hydroxy-5α-androst-16-ene in boar saliva and 5α-andro-16-ene-3-one (androstenone) in boar fat. This group then tested and reported that androstenone acted as a pheromone to induce sexual behavioral responses in the estrus sow (Melrose et al., 1971; Booth et al., 1973). Melrose et al. (1971) reported that 59% of sows express estrus behaviors with no boar stimulation, 78% of sows expressed estrus with an androstenone spray, but 97% of sows expressed estrus with fence-line contact with an adult boar. Thus, androstenone was not as good a stimulus as a nearby, live boar.

Androstenone was eventually used as an active ingredient in commercial products that are used to stimulate estrus behaviors in sows. However, the products were reported to stimulate some, but not all sows who are physiologically primed to express estrus behaviors. Doty (2010) cast doubt that androstenone was the only male pig sexual pheromone because the molecule did not elicit the full sexual behavioral response that a live boar induces (among other reasons). He also reported that pheromones might be a mixture of molecules rather than a single molecule. We, in this perspective hypothesized that the single molecule androstenone was not the complete pheromone of the adult male pig.

Our laboratory reported that the adult male pig has three unique volatile molecules in saliva namely: androstenol, androstenone and quinoline (May, 2016), for which a patent was also published (McGlone, 2016).

Wyatt (2010) suggested that mammalian pheromones may consists of 'signature mixture,' where each compound elicits a partial behavioral response but the mixture causes the synergistic behavioral responses in the responder animal. For instance, Karthikeyan et al. (2013) revealed the behavioral efficacy (eliciting flehmen and mounting) of a mixture of identified estrus-specific fecal compounds in buffalo were more effective compared to a single molecule.

The specific objective of this study was to determine the effects of each boar-unique molecule alone and in combination on sexual behaviors of sows. Sexual behaviors were measured in 947 sows on a commercial farm when exposed to a spray of each molecule or combination of molecules. We also sought to determine the individual behaviors and other signs of estrus in weaned sows, which were expected to express estrus.

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2. Materials and methods

2.1. General

All studies involving animals were approved by the Institutional Animal Care and Use Committee prior to conducting any animal work. All procedures were consistent with the Guide for the Care and Use of Agricultural Animals (American Society of Animal Science, 2010).

2.2. Evaluation of behavioral effects of individual and combinations of molecules

This study was a behavioral bioassay to determine if each boar-unique molecule alone or in combination caused sexual behaviors in sows who were weaned 4–5 days earlier. The goal was to evaluate about 100 sows per treatment in different air spaces; however, the sample size was variable among treatments based on the numbers of available sows in each air space (only one treatment was evaluated in one air space). The study was conducted in a large commercial pork production facility near Dalhart, TX where they keep over 50,000 breeding sows.

The boar-unique molecules were purchased as synthetic compounds from V.L. Clark Chemical, St Louis, MO (androstenone and androstenol) and Sigma Chemical, St Louis, MO. (quinoline). We tested eight solutions as a spray, including a vehicle control (ISO), three single active molecules (androstenone, quinoline, androstenol), three binary mixtures, (androstenone + quinoline, androstenone + androstenol, and androstenol + quinoline) and Boar Saliva Analog (BSA), which contained all three molecules. Each ingredient was added at a concentration of 10 μg/mL in isopropyl alcohol. Sows (n = 947) on day 4 or 5 post-weaning were randomly assigned and tested with the eight solutions in multiple barns (separate air spaces). Only a single evaluation was made in a given air space to avoid cross contamination. The significant distance between test barns avoided aerosol contamination among solutions. Research staff sprayed the solution on sow's snout (4 mL/spray with each sow receiving 40 μg of each molecule in a single spray). A preliminary study established a dose-response curve for the active molecules. Researchers used a mechanical sprayer in front of the crated sows while another person assessed estrus by back pressure test (BPT), while validating other behaviors (described below). This assessment was done between 0500 h and 0600 h (prior to workers arriving).

Behaviors recorded included: standing still (rigid), standing moving/shifting positions, head still or moving, pricked or erect ears, lordosis (arched back), vaginal mucus secretion, scratching (the floor or bars), and vocalizations (Table 1). The key behavior that stock people use to determine estrus behavior is standing still. We performed Pearson correlation calculations to determine the degree to which each other behavior was correlated with standing still. Behaviors that were highly correlated with standing still were not included in the sexual behavior score because they were essentially measuring a similar, correlated behavior.

A sexual behavior score was developed by summing three key individual behaviors (standing still, lordosis and pricked ears) into a single sexual behavior score. Both raw means and percentage response relative to the ISO-treated sows were calculated. Data from sows expressing each behavior, vocalizations and vaginal mucus secretion were analysed by Chi-square relative to the behaviors or responses of ISO-treated sows. Other Chi-square analyses determined if each treatment differed from BSA values.

2.3. BSA effects on onset of estrus in weaned sows

To determine if treatments induced changes in sexual behaviors or their timing, BSA was used on 122 sows (BSA (n = 70) ISO controls (n = 52) on two post-weaning days (days 4 and 5). Sows were weaned on the same day but placed in one of two rooms of breeding crates (different air spaces, but identical wean date, genetics, nutrition and housing). BSA-treated sows experienced 4 mL of BSA and 4 h later they were exposed to the boar as the boar walked in the aisle by the crated sows. The sows that had only boar exposure plus a placebo spray of ISO served as a control group. On day 4 post-weaning, only some sows are normally in estrus. By day 5, sows are expected to naturally express estrus behaviors. Investigators and farm staff examined the estrus behaviors with a boar in the aisle 4 h after spraying the sows with either BSA or a placebo, and if estrus was expressed, sows were artificially inseminated. The percentage of sows expressing behavioral estrus on days 4 and 5 were compared for BSA and ISO-treated sows by the farm staff who were blind to treatments. Sows were examined for pregnancy by farm staff 35 days after artificial insemination using ultrasound scanning. Chi-square analyses were used to determine if treatments differed on each post-weaning day.

3. Results

3.1. Evaluation of behavioral effects of individual and combinations of molecules

Behavioral and other signs of estrus were determined while the back pressure test (BPT) was applied. A sow was considered to be in estrus when she would submit to aritifical insemination by farm staff. The average values for the seven responses are shown in Table 1. Five responses were behavioral, and the two additional responses included were vocalizations and a thick vaginal mucus secretion associated with estrus. Less than 20% of estrus sows had a thick, sticky vaginal mucus discharge/secretion (Table 1). About 40% of sows vocalized while

Table 1
Definitions and abbreviations of behavioral measures, and percentage of sows expressing each measure.

Measure	Definitions	Average % of control sows expressing each measure
BPT	Back pressure test. Person stands behind sow and places and moves hands firmly on the middle of each sow's back.	n/a
Standing still	The sow is motionless, with contracting, rigid limbs during or after BPT was applied	71.1%
Moving	The sow is moving during or after the BPT (usually away from the research staff)	29.7%
Pricked ears	The sow has ears that are erect during or after application of the BPT	36.1%
Lordosis	The sow has an arched back upward, tensed shoulders, and legs apart, tense during or after application of the BPT	31.6%
Mucus	The sow has a thick, white mucus secretion/discharge from the vulva	19.8%
Scratching	The sow is scratching itself during or after the BPT (usually against the bars)	17.0%
Vocalizations	The sow vocalizes (grunt or squeal) during the BPT	40.5%
AN	5α-androst-16-ene-3-one (androstenone)	
AL	5α-androst-16-en-3α-ol, synonym: 3α-Hydroxy-5α-androst-16-ene (androstenol)	
Q	1-Benzazine, 2,3-Benzopyridine (quinoline)	
BSA	Boar Saliva Analog; a mixture of AN + AL + Q	

Table 2
Response of sows to the back pressure test (BPT) upon exposure to different treatment solutions.

Treatment solution	Number sows	% Standing still	% Pricked ears	% Vocalization
BSA	88	86.4%	52.3%	76.1%
Androstenol	87	78.2%	32.2%	46.0%
ISO-control	116	73.3%	36.2%	41.4%
Androstenone + Androstenol	111	67.6%	27.9%	43.2%
Androstenol + Quinoline	194	60.8%	66.0%	69.6%
Androstenone + Quinoline	74	52.7%	23.0%	45.9%
Androstenone	59	52.5%	45.8%	66.1%
Quinoline	218	49.5%	69.7%	84.4%
Total number of sows	947			
Higher than ISO Control, $P < 0.05$		BSA	BSA, Q, AL + Q	BSA, Q, AN, AL + Q,
Lower than ISO Control, $P < 0.05$		AN, Q, AN + Q	AN + Q	–

applyig the BPT. The behavior expressed at the highest level was standing still, also referred to as the standing or immobility reflex (indicative of sows being in estrus). Not all sows showed all behaviors associated with estrus.

Table 2 shows the percentage of sows that expressed standing still, pricked ears, and vocalization behaviors while the BPT was applied. Sows treated with BSA revealed a higher ($P < 0.05$) percentage of standing still behavior compared with ISO-treated sows. None of the other single molecules nor binary mixtures increased standing still compared to ISO. Furthermore, androstenone, quinoline and androstenone + quinoline-treated sows actually expressed lower ($P < 0.05$) standing still than ISO-treated sows. Pricked ears, were expressed only in about 28% of sows (Table 1). BSA, quinoline, and androstenol + quinoline caused higher ($P < 0.05$) levels of pricked ears compared with ISO-treated sows. Fewer sows receiving androstenone + quinoline expressed ($P < 0.05$) pricked ears than ISO-treated sows. BSA, quinoline, androstenol + quinoline and androstenone caused more sows to vocalise than ISO-treated sows. Sows undergoing the BPT and treated with any of the other (combinations of) molecules did not vocalize at a different rate than ISO-treated sows (Table 2). Considering these three behaviors, BSA caused all three responses at a higher rate than ISO ($P < 0.05$). While quinoline casued increases in pricked ears and vocalizations, it caused a lower percentage of standing still.

Correlation coefficients among measures of sexual behaviors with standing still were calculated (Table 3). Sows given the BPT that expressed standing still were negatively correlated (r = -0.92, $P < 0.01$) with moving. While none of the other correlation coefficients were significantly different from zero, their direction provided information about which behaviors were increased or decreased relative to standing still.

A simple sexual behavior score was constructed and included the score values for standing still, pricked ears and vocalizations behaviors. The score was presented relative to the score for sows experiencing ISO-treatment (Fig. 1). Sows treated with androstenol alone did not differ from ISO-treated sows. Androstenone + androstenol and androstenone + quinoline caused a lower ($P < 0.05$) sexual behavior score than sows experiencing the ISO- treatment, whereas all other solutions (single, binary mixture and BSA) increased the sexual behavior score compred with the ISO-treatment. Interestingly, androstenone caused a 13.5% higher sexual behavior score ($P < 0.05$) than ISO-treatment, but not as high as several others, and especially BSA that cuased a 63.9% increase ($P < 0.01$) in sexual behavior score than ISO-treatment.

The behavioral and other responses were put in a simple table to show which molecules alone or BSA caused increases or decreases in each average response (Table 4).

Sows treated with BSA had a greater ($P < 0.01$) probability of sows expressing behavioral estrus on d 4 after weaning compared with sows experiencing ISO. Pre-spraying with BSA 4 h before estrus detection caused more sows to express behavioral estrus on day 4 after weaning. On day 5 after weaning, a higher percentage of sows expressed estrus among ISO-treated sows compared with BSA-treated sows (Table 5). Ultrasound scanning 35 days later showed that 100% of all BSA- and ISO-treated sows were pregnant.

Table 3
Pearson correlation coefficients between standing still (the single most definitive sexual behavioral response) and measures of other sexual behaviors. Each value in the correlation calculation was the average response for each of the 8 molecules (7 df).

Behavior	R-value	P-value
Moving	−0.92	< 0.01
Lordosis	0.56	> 0.10
Vaginal mucus discharge	0.53	> 0.10
Pricked ears	−0.21	> 0.10
Vocalizations	−0.22	> 0.10
Scratching bars	−0.25	> 0.10

4. Discussion

For decades androstenone was considered “the” boar pheromone, but it was recognized to not be as potent solely at induction of sow sexual behavior as a live boar (Signoret et al., 1975). The early literature is challenging to understand because the individual sexual behaviors that make up the standing reflex were not described. Moving and scratching behaviors of the sows are negatively correlated with standing still (Table 3). When sows expressed estrus, they stood still with their muscles contracted, sometimes to the point that their limbs were shaking. About one third (36%) of sows have pricked ears and vocalized (40%). Standing still, pricked ears and vocalizations are the key responses most associated with sexual behavior of the sow and were therefore, combined into a sexual behavior score.

Androstenone and androstenol were previously described in boar saliva. The success rate of androstenone and androstenol in an estrus detection model was (only) 58% and 54%, respectively (Reed et al., 1974). Quinoline has not been reported in boar saliva hitherto. Quinoline is a heterocyclic aromatic hydrocarbon molecule (it is not a steroid) used in defensive signaling of few insect species (Eisner et al., 1997). Urine of many animals, including rabbits, swine, and hens contain quinoline derivatives (Roy and Price, 1959; Kido et al., 1967) for reasons that are unclear. Quinoline is reported in the urine and anal gland secretions of the ferret (Zhang et al., 2005). Soini et al. (2005) found quinoline in the urine of adult male hamsters. Quinoline was also found in the feces of adult wolves (Martin et al., 2010) and secretions of African wild dogs (Apps et al., 2012).

Examination of the response of each molecule or combination of molecules tells us which molecules cause which behaviors at a higher rate than ISO-treatment. BSA caused a significant increase in the percentage of sows expressing all three key responses. Quinoline and androstenol + quinoline increased pricked ears and vocalizations in sows more than the ISO-treated sows (Table 2). Quinoline, on the other hand,

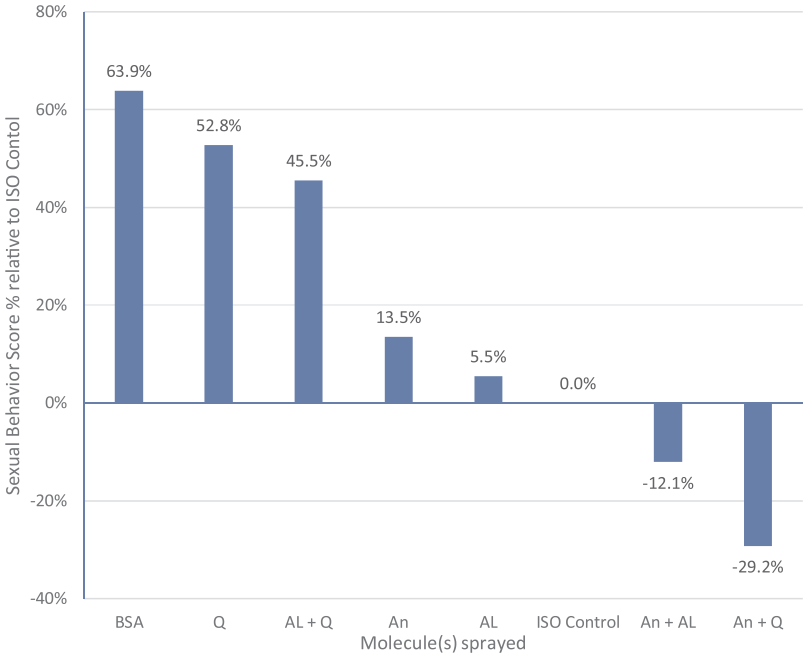

Fig. 1. The sexual behavior score sums the percentages of sows expressing standing still, erect ears, and vocalizations from Table 2. Percentage data in this graph are relative to the sexual behavior score of ISO control-treated sows which was set at zero. All percentages except Androstenol (AL) differ from the ISO control ($P < 0.01$) by Chi-square. A negative value represents a sexual behavior score lower than that observed for ISO control-treated sows. See Table 1 for definitions of abbreviations.

caused a significant reduction in standing still behavior compared to any other molecule(s). Two binary mixtures (androstenone + androstenol and androstenol + quinoline) had potential in inducing standing still, but none of the binary mixtures were effective in eliciting pricked ears or vocalizations as compared to any other molecules. It appears that the single molecules may differentially regulate sow behavioral responses. For example, giving just quinoline would increase pricked ears and vocalizations, but decrease standing still. Similarly, androstenone increased vocalizations, but decreased standing still. Giving any of the binary mixtures, for instance, androstenone + quinoline seemed to enhance some behaviors while decreasing others. Our data in Table 2 also supports the hypothesis that single molecules are not as effective (or can be negative) in the induction of sow sexual behaviors compared to when all three molecules are in the same solution (BSA). Further, variable concentration of each constituent to make BSA would be more promising.

The sexual behavior score provides an overview of the responses of weaned sows to a single molecule or combination of molecules. Androstenone did increase the sexual behavior score by 13.5% more than the ISO-treated sows. However, the highest sexual behavior score was resulted by BSA (Fig. 1). The sexual behavior score of BSA-treated sows was over 50% higher than androstenone alone (63.9 vs. 13.5%, $P < 0.05$ by Chi-square). Through this, we affirmed that BSA is the most potent solution to induce sow sexual behaviors among the boar-unique molecules tested.

The field study conducted was an attempt to document if BSA can induce sexual behaviors in sows after weaning. Many, but not all, sows begin to express estrus 4 days after weaning. A pre-spray with BSA caused more sows to express estrus on day 4 compared with day 5 after weaning (Table 5). In all cases, these behavioral tests were performed with boars in the barn and often in the aisle in front of sows when farm staff was checking estrus among weaned sows.

Table 5
Percentage of 122 sows expressing behavioral signs of estrus on days 4 and 5 after weaning. Sows were treated with Boar Saliva Analog (BSA; n = 70) or ISO-control (n = 52) 4 h before farm staff (who were blind to treatments) assessed estrus in sows. Chi-square analysis of % sows in estrus was highly significant ($\chi^2 = 42.26$, $P < 0.01$).

Treatment	Number of sows included		% Sows in estrus	
	Day 4	Day 5	Day 4	Day 5
BSA	44	26	63.6%	23.1%
ISO	41	11	19.5%	63.6%
Total	85	37		

BSA spray caused more sows to express estrus behaviors on day 4 than use of a boar alone (Table 5). Functionally, this means that the wean-to-estrus interval would be less on average with BSA-treated than control sows. We believe that the BSA is a stronger signal and so it may bring out expression of sexual behaviors that would not otherwise be observed that early.

This study was not designed to determine if BSA was equal to a boar in the initiation or overt expression of sexual behaviors in weaned sows. Further experimentation will have to determine if the live boar can be replaced by this more complete boar pheromone. We also found an increase in sow alertness when boar vocalizations were played for sows to hear (personal observation). However, the relative benefit of

Table 4
Significant changes in each measure compared with ISO-treated. Significance with $P < 0.05$ is labeled by a "+", and if a trend ($P < 0.10$) by the symbols ˜+. A negative sign (-) indicates this measure was significantly lower than ISO-treated. A blank cell indicates that measure was not different from ISO-treated.

ISO vs.	Behavioral or other measures						
	Standing still	Moving	Pricked ears	Lordosis	Mucus secretion	Scratching the bars	Vocalizations
Androstenone	–	+					+
Androstenol				–	+		
Quinoline	–	+	+				+
Boar Saliva Analog	+		+	˜+		–	+

supplementing boar audio to make this a more powerful chemical signal is unknown at this time.

In conclusion, we showed that the signature mixture of boar-unique salivary molecules (androstenone, androstenol and quinoline) induces sexual behaviors in sows after weaning. Further, the stimulatory sexual behavioral effect of BSA (containing all three active molecules) was more powerful than any single or binary boar-unique molecule(s). The most biologically-relevant boar pheromone seems to be a mixture of male-unique salivary molecules.

Author contributions

JJM supervised collection of the data, analyzed it, and revised the manuscript. SD performed bioassays, analyzed the data and edited the manuscript. AG assisted in the writing of the paper and in data collection. All authors reviewed and approved the final version of the manuscript prior to submission.

JJM is the inventor on the patent for this technology. JJM is an equity partner in Animal Biotech, LLC who funded these studies and licensed this technology from Texas Tech University (the owner of this intellectual property).

Declaration of Competing Interest

JJM is the inventor on the patent for this technology. JJM is an equity partner in Animal Biotech, LLC who funded these studies and licensed this technology from Texas Tech University (the owner of this intellectual property).

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References

Apps, P., Mmualefe, L., McNutt, J.W., 2012. Identification of volatiles from the secretions and excretions of African wild dogs (Lyacon pictus). J. Chem. Ecol. 38, 1450–1461.

Booth, W.D., Mary, F.H., Dott, H.M., 1973. Sexual dimorphism in the submaxillary gland of the pig. J. Reprod. Fert. 33, 163–166.

Doty, R.L., 2010. The Great Pheromone Myth. Johns Hopkins University Press, Baltimore, MD.

Eisner, T., Morgan, R.C., Attygale, A.B., Smedley, S.R., Herath, K.B., Meinwald, J., 1997. Defensive production of quinoline by a phasmid insect (Oreophoetes peruana). J. Exp. Biol. 200, 2493–2500.

Karthikeyan, K., Muniasamy, S., SankarGanesh, D., Achiraman, S., Ramesh Saravanakumar, V., Archunan, G., 2013. Fecal chemical cues in water buffalo that facilitate estrus detection. Anim. Rep. Sci. 138, 163–167.

Kido, R., Noguchi, T., Tsuji, T., Matsumura, Y., 1967. The identification of 4,6-Quinolinediol and 4,8-Quinolinediol in the urine of hens. Biochim. Biophys. Acta 136, 131–135.

Martin, J., Barja, I., Lopez, P., 2010. Chemical scent constituents in feces of wild Iberian wolves (*Canis lupus signatus*). Biochem. Syst. Ecol. 38, 1096–1102.

May, M., 2016. Use of Solid-Phase Microextraction to Detect Semiochemicals in Synthetic and Biological Samples. M. S. Thesis. May, 2016. Texas Tech University. https://ttu-ir.tdl.org/ttu-ir/bitstream/handle/2346/67038/MAY-THESIS-2016.pdf?sequence=1.

McGlone, J.J., 2016. Pheromone composition to stimulate reproduction in female suids and methods of use. USA patent US9480689B1. Published on Nov 11, 2016.

Melrose, D.R., Reed, H.C., Patterson, R.L., 1971. Androgen steroids associated with boar odour as an aid to the detection of oestrus in pig artificial insemination. Br. Vet. J. 127, 497–502.

Patterson, R.L.S., 1968a. Identification of 3α-hydroxy-5α-androst-16-ene as the musk odor component of boar submaxillary salivary gland and its relationship to the sex odor taint in pork meat. J. Sci. Fd. Agric. 19, 434–438.

Patterson, R.L.S., 1968b. 5α-andro-16-ene-3-one:- compound responsible for boar taint in boar fat. J. Sci. Fd. Agric. 19, 31–38.

Reed, H.C., Melrose, D.R., Patterson, R.L., 1974. Androgen steroids as an aid to the detection of oestrus in pig artificial insemination. Br. Vet. J. 130, 61–67.

Roy, J.K., Price, J.M., 1959. The identification of quinoline derivatives obtained from the urine normal rabbits and swine. J. Biol. Chem. 234, 2759–2763.

Signoret, J.P., Baldwin, B.A., Fraser, D., Hafez, E.S.E., 1975. The behavior of swine. In: Hafez, E.S.E. (Ed.), Behaviour of Domestic Animals. Bailliere Tindall, London, pp. 295–329.

Soini, H.A., Weisler, D., Apfelbach, R., Konig, P., Vasilieva, N.Y., Novotny, M.V., 2005. Comparative investigation of the volatile urinary profiles in different Phodopus hamster species. J. Chem. Ecol. 31, 1125–1143.

Wyatt, T.D., 2010. Pheromones and signature mixtures: defining species-wide signals and variable cues for identity in both invertebrates and vertebrates. J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol. 196, 685–700.

Zhang, J.X., Soin, H.A., Bruce, K.E., Wiesler, D., Woodley, S.K., Baum, M.J., Novotny, M.V., 2005. Putative chemosignals of the ferret (Mustela furo) associated with individual and gender recognition. Chem. Senses 30, 727–737.