Chapter

Understanding Sow Sexual Behavior and the Application of the Boar Pheromone to Stimulate Sow Reproduction

John J. McGlone, Edgar O. Aviles-Rosa, Courtney Archer, Meyer M. Wilson, Karlee D. Jones, Elaina M. Matthews, Amanda A. Gonzalez and Erica Reyes

Abstract

In this chapter, we review the sexual behavior of domestic pigs, and the visible or measurable anatomical features of the pig that will contribute to detecting sows in estrus. We also summarize olfactory organs, and the effects of a sexual pheromone on pig's biology and sow reproductive performance. We discuss the role of a live boar in the heat detection where the female is in breeding crates. However, there is an increasing interest in being able to breed sows without a boar present. Farm workers must be trained on the fine points of estrus detection so that they can work in a safe and productive setting. After a review of olfactory biology of the pig, the chapter explains how new pheromonal technology, such as BOARBETTER®, aids in the process of heat detection with or without a live boar. To achieve reproductive success, the persons breeding must assimilate all fine points of pig sexual behavior and possess a clear understanding of what they should be looking for in each sow they expect to breed.

Keywords: pigs, reproduction, sexual pheromone, sexual behavior

1. Introduction

In 2018 the world had over 700 million pigs with over half of them in China [1]. With the recent spread of African Swine Fever (ASF) in China and other parts of Asia, the pig population has rapidly declined. At the same time, movement of breeding animals is restricted in the most pig-dense continent and so rebuilding pig numbers is a challenge. When diseases like ASF break out, and breeding animal movement is restricted, then some sows must be bred without the use of adult males. Successful pig breeding is the key to maintaining and restoring pig numbers and the world's supply of pork.

In cattle herds and poultry flocks, successful breeding often takes place without any adult males. In contrast, most commercial pig farms have adult male pigs (boars) on site to maintain optimum breeding success. Thus, the pig is unique among common food animals in requiring the presence of adult males in

Figure 1.
Outdoor systems with natural mating (left) are less common today. Sow in a breeding crate or stall (right). The breeding crate is the most common indoor breeding system. Note that in the outdoor, natural mating system, the sow and boar can fully interact. However, in the breeding crate, a person applies back pressure in the presence of a boar to induce sexual behaviors when a sow is in estrus. If the sow is not in estrus, she will not show sexual behaviors when the person applies pressure to her back.

commercial production. While some sows will express sexual behaviors without a boar, to get the majority of sows bred, in current commercial production, the male is thought to be required.

In less developed countries, pigs may roam free and are harvested as desired, but these represent a smaller percentage of the world pig inventory over time. Some commercial pigs are kept outdoors in managed systems. The outdoor production system (**Figure 1**, left) represents a small part of the world's pig herd. Most pigs in the world used for pork production are kept on commercial farms using an indoor sow housing system. The most common method of housing the breeding sow is in a crate or pen (**Figure 1**, right) [2]. The breeding crate is large enough (often 0.6 m × 2.1 m) to accommodate the body of the sow but the breeding crate does not allow the sow to turn around or to express her full repertoire of behaviors. The method of keeping breeding sows (outdoor, indoor in pens or crates) clearly impacts their ability to express natural sexual behaviors and the breeding crate reduces the likelihood of successful mating. Sexual behaviors are best observed in freely-moving sows and boars, but the reality of commercial pork production is that sows are in a breeding crate in which they may have limited fence line contact with an adult male—and this makes training of workers challenging. A better understanding by farm workers of sow and boar sexual behaviors will meaningfully improve reproductive success.

The objectives of this chapter are first to review the basic behavioral biology of sexual behavior and reproductive success in the domestic pig. Secondly, this chapter will summarize classic literature on sow and boar sexual behaviors and will review both applications of pheromone technologies and mechanisms by which pheromones can improve reproductive performance in the pig herd. To have a better understanding of pig sexual behaviors and of the impact of the boar sexual pheromone on female reproduction, we will also review pig olfactory system anatomy and physiology.

2. Sexual behavior in the domestic pig: early studies and preferred terminology

While pig farmers have observed sexual behavior for millennia, the earliest scientific description of sow sexual behavior in the scientific literature was in 1941 by Altmann [3]. Altmann was a psychologist at the University of Chicago when animal behavior was developing in the USA. Altmann studied female pig sexual behavior because she used pigs in her conditioning studies, and she wanted to be sure if sows were or were not in heat when she trained them on an operant task. In 1941, she reported several aspects of sow sexual behavior that we know to be true. She said there was a 18–23 day cycle among adult females. She indicated that domestic sows (unlike wild boar) bred year-round, although they often had a "silent heat" in warm weather. She found external signs of estrus to be not reliable indicators of estrus; these included, vaginal mucous, swelling of the vulva and rectal temperature changes. We recently confirmed her observations with quantification of anatomical changes (see below). She indicated behavior and activity were the best methods to determine heat, but a combination of methods increased accuracy.

The next scientist to publish studies in pig sexual behavior was Jean Pierre Signoret from France. His research on sow sexual behavior in the 1960s and early 1970s were summarized in a chapter Signoret co-wrote in Hafez's 1964/1968/1975 editions of the book "The Behaviour of Domestic animals" [4]. The picture of sow-boar sexual behavior in that chapter has been widely used to describe pig's sexual behavior. In that picture, he lists sequences of boar-sow behaviors that are shown in **Figure 2**. The sequence of sexual behaviors between a sow and boar include mutual head sniffing, and then the boar sniffs the sow's rear, he then pushes and may lift the sow from the side, then he sniffs and licks and pushes on the sow's rear. These olfactory and tactile behaviors are accompanied by grunting by the boar and, if the sow is in estrus, she will be silence or she will make soft rhythmic grunts in response (she will squeal if she is not in estrus as a form of objecting to the boar behavior). After touching, smelling and licking her rear, he will mount her and if she is fully in estrus and showing "standing reflex or locked up" behavior, he will copulate with her.

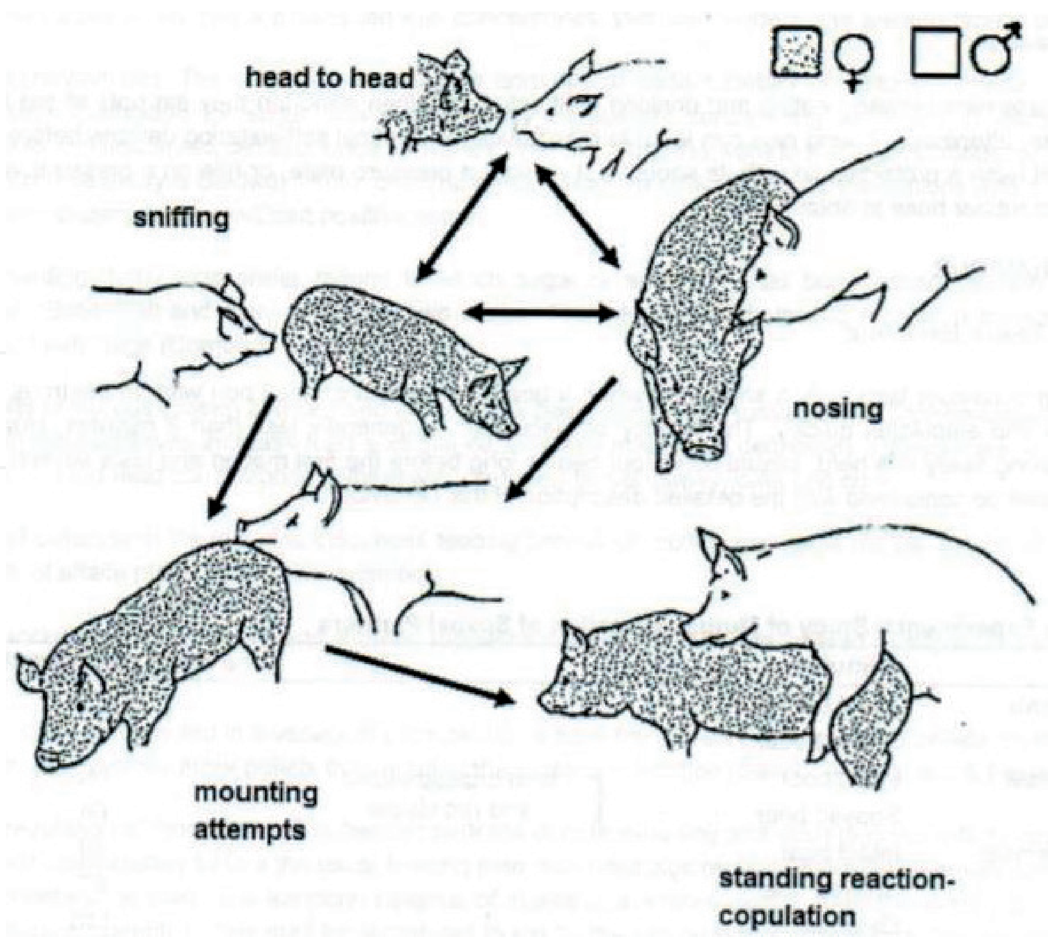

Figure 2.
Drawings of sow-boar sexual behaviors from Signoret [4].

We present in **Table 1** our definitions of sow sexual behaviors that are observed while a sow is in a breeding crate. Note that because her movements and boar interaction are restricted while in a breeding crate, she will not express the same number of behaviors as in the wild. When the sow expresses intense standing still, we say she is "locked up." A sow can stand still for a few seconds at any time and not be locked up or in estrus. Being locked up is the primary and only reliable sign that a sow is in estrus.

The boar is non-discriminating when deciding which animal or object to mount. The boar will attempt to mate sows not in estrus and they will mate an object shaped roughly like a sow (e.g., a boar semen collection dummy)—anything shaped like a cylinder that stands still will be mounted by an adult boar.

If the sow is not in full estrus, she will avoid the boar. If she experiences an adult boar while not in heat, then she will vocalize (squeal) and be aggressive towards him to express her objection. In the author's personal observations of feral pigs and outdoor pigs allowed to mate naturally, a sow not in estrus is very aggressive towards adult males. With the matriarchal social structure in nature, the sow is clearly dominant to the boar, except when she is in estrus.

In the period of proestrus, the sow is becoming interested in the boar, but she will still not be willing to stand still for mounting. In this period, she will seek a boar, interact with him and allow for mutual sensory exploration. When these behaviors are observed and the BPT is administered, the sow will not stand still. This period is referred to on the farm as a sow that is coming into estrus but not fully in estrus (proestrus).

Word	Definition
Standing still	Also called standing posture, the sow is motionless for intervals no greater than 10 consecutive seconds
Standing reflex, locked up	When a sow stands still for more than 10 consecutive seconds, usually by applying back pressure. This behavior is exhibited by sows when they see the boar, during the back-pressure test, or when being mounted. Sometimes displayed together with pricked ears and muscle contraction (rigid muscles and in some sow muscle shaking)
Latency to lock up	Time in seconds from application of back pressure until the sow locks up. When a sow is in estrus, latency is usually less than 30 s
Pricked ears	Lifting ears from resting position, usually while sniffing and exhibiting sexual interest. Ears either stand straight up or are obviously higher than resting
Moving	Before and after full estrus, sows will move when back pressure is applied
Sniff	When a boar is near or when they experience a pheromone, they move their rooting disk as they sniff (see videos)
Chomping	When the sow has nose-to-nose contact with a boar, or if they experience the complete pheromone, they will open and close their mouth, and move their tongue in and out while they keep their head level or elevated so they can apply the liquid to their VNO
Vocalization—stress	Sows express a high-pitch squeal when they are objecting to back pressure or a boar. This is a stress vocalization sows make when are not in estrus
Vocalization—"chatting" or "chanting" with the "boar"	The sow grunts in a low-pitch repeated manner when she sees, smells or hears a boar. This vocalization is not expressed by all sows

We use these and related definitions in our recent work.

Table 1.
Definitions of sow sexual behavior when she is in estrus.

In a breeding crate, the most noticeable sexual behaviors expressed by a sow are locked up and pricked ears (see **Table 1** for definition). Stock people that breed sows will be familiar with these sexual behaviors. However, we recognize that there is considerable variation in sexual behaviors within genetic lines and among genetic lines (and breeds). Some individual sows show more extreme sexual behaviors and some show only mild signs of being in estrus. Video in the following link (https://youtu.be/DdgxK1U8ZUo) shows a sow with a strong sexual behavioral response after boar exposure. Video in the following link (https://youtu.be/tspB7RkviBo) shows the same sow that expresses sexual behavior after application of the new boar pheromone [5]. Note the locked up behavior, sniffing and chomping by the sow.

Commercial farms must train workers who perform artificial insemination (AI). Pig breeders must understand sow sexual behavior to achieve success. With training and experience, the AI technician can achieve very high breeding and farrowing rates, but rarely 100% of sows are bred and remain pregnant. Training workers is challenging because sows vary widely in their sexual behaviors. AI workers must be trained with the specific genetic line of pig they are expected to breed. They must understand what normal sexual behavior is for that genetic line and then how to modulate that behavior to achieve high levels of reproductive success. Training is challenging because sows in breeding crates are not able to express the full repertoire of sexual behaviors that they express in an open area and boars are not able to stimulate crated sows through olfactory and tactile senses as they can for penned or pastured pigs.

3. Overview of the estrus cycle

3.1 Hormonal changes

The sow estrus cycle is of 18–24 days long [6], with the median and mode of 21 days. Sows are polyestrous animals. This means that with the appropriate nutrition, good health, and the proper environmental conditions, sows will cycle through the year. The sow estrus cycle is only stopped by pregnancy or lactation, and possibly old age. In sows, lactational anestrus is due to the inhibition of the GnRH pulse by the suckling stimulus [7]. Gilts reach puberty at 5 or 6 months old. For sows, the first estrus post-weaning takes place 4–7 days after weaning for most, but not all sows (some have a longer or shorter wean to estrus interval).

During the estrous cycle, sow's hormones change. The hormonal changes mark the different stages of the estrus cycle. The sow estrus cycle is divided in two main phases, follicular and luteal. These phases are further divided into four stages. The follicular phase is divided into proestrus and estrus, while the luteal phase is divided into metestrus and diestrus.

For our discussion, we will assume that the first day of estrus is day 0 of the cycle (**Figure 3**). The onset of estrus is mainly caused by an increase in estrogens. Sow estrus usually last 40–60 h (from day 0 to day 1–2 of the cycle) [6] but some sows can be on estrus for longer. Sow will only show sexual behaviors and accept the boar during the estrus stage of the cycle. During estrus, estrogen, Follicle stimulating hormone (FSH) and Luteinizing hormone (LH) secretion peaks. During estrus, ovulation is caused by the LH surge. Ovulation occurs 30–40 h after estrus onset [6].

Almost immediately after ovulation, sow will enter the luteal phase. During the metestrus stage of the luteal phase (days 2–5 of the cycle), the follicle tissue will start its development into a corpus luteum. This process is called luteinization [6]. The end of metestrus and the beginning of diestrus is marked by the end of the

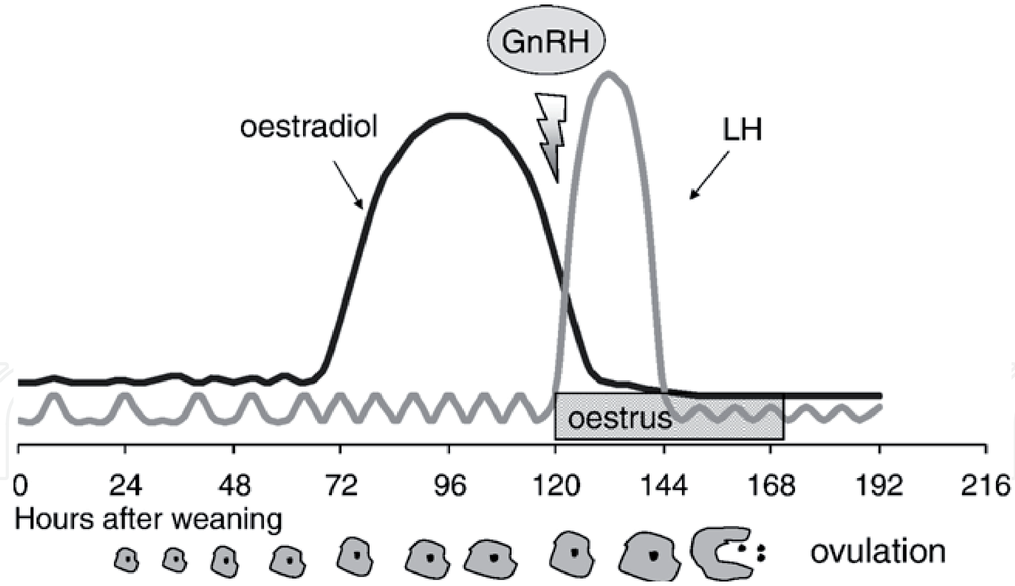

Figure 3.
Schematic of the timing of ovulation with associated hormonal and behavioral changes. Weaning is at time zero. From Pedersen [8].

luteinization process. Diestrus is the longest stage of the estrus cycle. It starts once the corpus luteum is formed and last for 12–15 days after (days 6–17 of the cycle). The corpus luteum will secret progesterone to prepare the uterus for implantation and to maintain pregnancy in case of successful fertilization by the boar or artificial insemination. If the sow is not pregnant, the uterus will start secreting prostaglandin F2 alpha and luteolysis (degradation of the corpus luteus) will start after 15 days post ovulation (proestrus stage) [6]. Proestrus (day 17–21 of the cycle) is characterized by an increase in prostaglandin F2 alpha secretion and the completion of luteolysis. During this phase, progesterone secretion is reduced and estrogen, then LH, and FSH secretion increase. This increase will re-start estrus.

3.2 Anatomical changes (vulva size, color, and temperature)

The introduction of assisted reproductive techniques, such as Artificial Insemination, has shifted the responsibility of estrus detection to humans with the assistance of a live boar. The traditional way to identify if a sow has come into heat and is ready to be breed, is based on the occurrence of sexual behaviors before, during or after the backpressure test (BPT) and by detecting physical changes in sow vulva. Physical changes associated with the onset of estrus are reported to include vulva reddening, increase in vulvar temperature, the presence of sticky mucus, and an increase in vulva size often refer as swelling.

Langendijk et al. [6] found that out of 130 sows only 87% showed an increase in internal vulva redness. In this study, they also found a significant variation on the time vulva reddening occurred. Even when reddening onset varied between individual sows, it always occurred before ovulation. Thus, they suggest that insemination of sows that shows vulva reddening should be delayed until the end of vulva reddening.

The increase in vulva size and infrared temperature observed during estrus have been correlated to the high estrogen levels during estrus. The elevated levels of estrogen increase the vaginal and vulvar blood flow resulting in both an increase in vulva temperature as well as vulva swelling [9]. The literature is contradictory related to vulva features. Sykes et al. [9] and Scolari et al. [10] found that the infrared vulva temperature increased by 1 C° the day of estrus whereas Simoes et al. [11] found that the temperature increase was during the proestrus period.

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Un-published studies recently conducted by the authors showed that not all sows will show these physical changes. We carefully measured color, size, surface temperature and vaginal temperature in sows before and during estrus (**Table 2**). Sows might show these physical changes at a different stage of the estrus cycle. Because not all sows will show changes in vulva color, temperature, or size during estrus, the onset of these changes varied among individual animals. Vulva physical and thermal changes are not reliable indicators for heat checking for all sows of use on the farm.

3.3 Skeletal and smooth muscle contractions

Myometrial activity before and after estrus is either absent or of low amplitude and frequency [12, 13]. During estrus, sow myometrial electrical activity and contraction frequency and amplitude increase [12]. Myometrial contractions are regulated by progesterone, oxytocin, and estrogen concentrations [14]. High progesterone reduces uterine contractions whereas high oxytocin and estrogen levels increase them [14]. Oxytocin and estrogen secretion increase during estrus and sexual stimulation and arousal, although direct neuromuscular activation could be via the brain and spinal nerves. In vitro studies found that after an estrogen perfusion, there was a significant increase in peristalsis going from the isthmus uteri towards the corpus uteri [15]. Similar results were found with an oxytocin perfusion [15]. Uterine contractions are necessary for the movement of sperm from the uterus to the fallopian tubes. This could explain why seminal oxytocin and estrogen increase uterine contractions [12]. Boar presence induces sow oxytocin release and increases sow's myometrial activity [12]. The effects of each individual boar stimulus (olfactory, tactile, and visual) on oxytocin release are still not clear [12].

Some sows will also show skeletal muscle contraction that one would call shaking during the standing reflex. From our behavioral studies, we estimated that fewer than one in ten sows will show this behavior. Skeletal muscle movement can be easily perceived on sow shoulders, flank, neck and ears.

3.4 Gilt development

To continue the production cycle and swine sustainability, sows need to be replaced by gilts. Breeding farms should target to have an annual replacement rate lower than 50% [16]. In 2012, the average annual replacement rate was 45% [17]. This mean that around 900 gilts are needed per year to replace culled sows in a 2000 sow unit. Usually sows are culled due to low reproductive performance, lameness, or because they were not bred after weaning.

Measurement	Day when the change was visible			
	Day before estrus	First day of estrus	Day after first day of estrus	No change
Vulva reddening	31.82%	18.18%	13.64%	36.36%
Vulva IR temperature	4.55%	59.09%	9.09%	27.27%
Vaginal temperature (C°)*	0.00%	15.38%	0.00%	84.61%
Vulva swelling	31.82%	13.64%	0.00%	54.55%
Presence of sticky mucus	40.91%	36.36%	22.73%	0.00%

The percentage figures refer to the % of sows that first show that feature on each day.
**n = 13.*

Table 2.
Proportion of sows (N = 22) that showed vulva changes before, during, or after the first day of estrus.

Replacement gilts are selected based on their growth rate, body composition, and their mother's reproductive success [17]. In general, gilts selected as replacement are moved from the growing facility to the gilt development unit (GDU) within the breeding farm when they are around 150 days old. To accelerate the onset of puberty, gilts in the GDU are often exposed to live boars. Gilts can have direct contact with a boar or indirect contact through pen fencing. Usually, groups of vasectomized boars are introduced into gilt's home pen for at least 20 min per day. Boar should not be housed in the GDU unit since gilts will be habituated the boar olfactory, visual, tactile, and auditory stimuli and this could decrease effective heat detection by farm workers [17].

When boars are introduced into the gilt pen, farm personnel will check gilts for estrus behavior and vulva changes described above. Daily boar exposure will induce estrus in most gilt within 10–20 days [17]. Gilts in heat are then moved to breeding stalls so they can habituate to the new environment and are breed in their second estrus. The term heat-no service (HNS) is commonly used to identify gilts that had their first estrus but were not breed. At the time of first service gilts should weight 135–150 kg and have a back fat of 12–18 mm [16, 17]. After 23 days of boar exposure, gilts that have shown no sign of estrus, can be hormonally treated to induce estrus by use of PG600. Gilts that did not come into heat after 28 days of boar exposure are usually culled from the breeding herd [16]. Gilts can be treated with Altrenogest to synchronize their estrus cycles.

4. Sensory system impacts on the estrus cycle: the boar effect

4.1 The boar effect

The effect of boar exposure on gilts and sow reproduction has been extensively study across the years. Direct contact with the boar significantly reduces puberty onset in gilts [18–22] and reduce sows weaning to estrus interval. The boar provides sows and gilts with olfactory, tactile, visual, and auditory stimuli that together create a maximum response. Below we discuss the effect of each individual boar stimuli on sow and gilt reproduction.

4.2 Visual, auditory and tactile systems

Pigs have well developed olfactory, tactile, auditory and visual systems. Most of the work on the pig focuses on the pig olfactory sense. Pigs have been used in biomedical research to study the auditory system. The auditory and somatosensory (touch) parts of the brain have been mapped in the pig [23]. The pig auditory system is understudied. In one paper where the auditory, visual and somatosensory regions were mapped in pig reared indoors or outdoors, the authors showed different neuron structures in the outdoor pig in both auditory, visual and somatosensory regions [24]. The auditory neocortex was especially different with diverse housing systems.

Surprisingly few recent studies have been done on the pig visual system. Dudley Klopfer was a psychologist at Washington State University in the 1950s to about 1980. He studied the pig visual system using operant conditioning methods. He found that pigs could see colors. His work was published in a detailed proceedings paper in 1966 [25]. Ewbank [26] and his group put black contact lenses on pigs which made them temporarily blind. Pigs that could not see, had normal fights and formed a dominance hierarchy. In the world, pig do not need their sight to function, even though their eyesight is about the same as humans.

What we can conclude from the limited work on pig senses is that their olfactory system is much more developed than humans (see below) and their auditory, visual and somatosensory systems are at least as developed as humans.

4.3 Olfactory systems

Meese and Baldwin [27] removed the olfactory bulbs in pigs and this did not change their establishment of a dominance order. When pairs of pigs were tested, they fought the same with or without their olfactory bulbs. However, when the group size increased to 3 or 4 pigs, the bulbectomized pigs were at a disadvantage. For reproduction, removal of the olfactory system had large negative effects on reproduction [28].

The boar olfactory stimulus has been widely studied of known mammalian pheromones. During the 1960s, androstenol (5alpha-Androst-16-en-3alpha-ol) and androstenone (5alpha-Androst-16-en-3-one), two steroids secreted by boars' submaxillary salivary glands, were thought to be the boar pheromone. Multiple studies have found that these two steroids have a major role on gilts puberty onset. For instance, puberty age was significantly greater for gilts with their olfactory system inhibited by chemical or mechanical means [29, 30] and for gilts exposed to a sialectomized boar [31]. It is thought that direct contact between boar and sow is necessary to transfer the boar pheromone from boar saliva to the female snout [30]. Although these two steroids are responsible for a significant part of the boar effect on puberty onset, when applied as an individual olfactory stimulus, they were not as effective as the boar [18, 21]. Thus, it was suggested that boar saliva must contain additional analytes that together with androstenol and androstenone are acting as a multicomponent primer pheromone or that other boar stimuli are necessary for the boar pheromone to have a full effect. Recently, it was found that, quinoline was another boar specific salivary molecule (**Figure 4**) [5, 32]. The mixture of androstenone, androstenol, and quinoline induced more sexual behaviors in weaned sows than the mixture of androstenone and androstenol [5]. This finding might explain the lack of response of sows and prepubertal gilts when exposed to androstenone and androstenol alone.

4.4 Early work on sow and boar preferences and sensory systems

Boars, being a non-discriminating breeder, will investigate sows independent if they are in estrus or not but sows will only be interested in a boar when they are in estrus. When sows are in Proestrus, they will seek a boar. This seeking behavior intensifies when sows are fully in estrus.

Early works showed that sows would only seek the boar when they are in estrus [33] and that the boar could not detect a sow in estrus. This turned out to be only partially correct. Boars can learn the smell of an estrus sow. It was reported that the boar could not tell an estrus sow from a non-estrus sow [32, 34]. Some boars were found to be able to find an estrus sow while others could not [32, 34]. This could be a learned behavior, or some boars may have better olfactory acuity than other boars. This remains to be determined.

Signoret's classic early research [4] (**Table 3**) on boar induction of sow sexual behavior is often cited in textbooks and seminars. In his work, he found that the boar odor was the best single stimulus to induce sexual behaviors in estrus sows. He applied back pressure to estrus sows with no odor stimulation and found that 59% of the sows showed standing reflex. If farms found only 59% of the sows that are in heat, they would not be profitable. The goal is to find 100% of the sows in estrus. With a live boar across a fence, Signoret found that 97% of the sows were detected

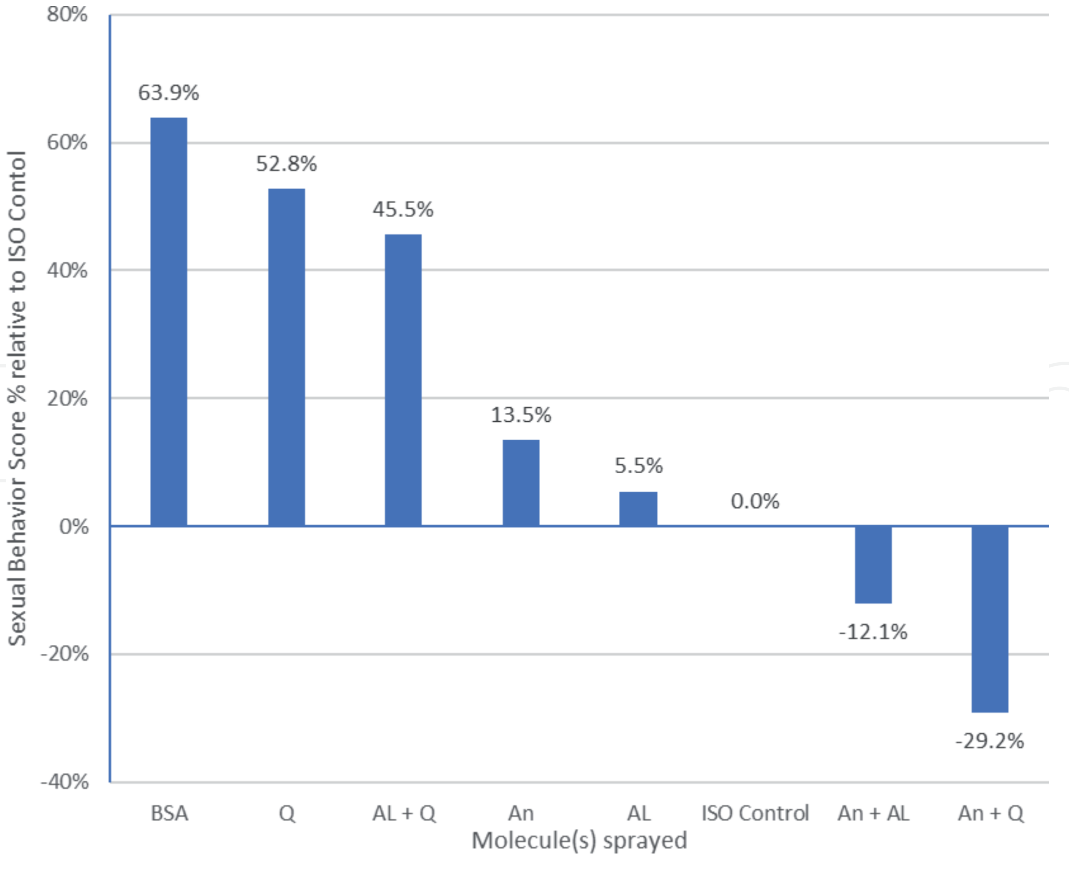

Figure 4.
Sow sexual behavioral response to Androstenone (An), Androstenol (AL) and Quinoline (Q) alone or in combination. Note that androstenone increased estrus sow sexual behavior by 13.5% while all three molecules increased sow sexual behavior by over 63%. The N for this study was 947 sows [5].

Source	Odor source	Sows showing estrus
Signoret, 1975 [4]	No boar odor	59%
	Boar odor in pen	81%
	Fence-line contact with live boar	97%
Melrose [35]	Androstenone	78%*
Note that Androstenone (*) was not as effective as fence-line contact with a boar.		

Table 3.
Early research on sensory system impacts on sows showing estrus.

in estrus. Further, he found that 81% of sows were detected in estrus when they were moved and heat checked in a pen containing the boar odor. This is better than 59%, but not as good as the live boar. Later, when Androstenone was used, Melrose [35] found 78% of the sows in heat—similar to Signoret's finding with the boar odor. Scientists and producers thought at that time that Androstenone was the boar pheromone. However, why would the fence line contact be better than the odor of the boar or Androstenone alone? This is because more than Androstenone (e.g., other molecules) is needed to induce sexual behavior in the sow (see details below).

5. The pig olfactory system

The pig is a species with one of the highest numbers of functional olfactory genes [36]. To understand pig pheromone biology, one must understand the different olfactory organs of the pig. Only two of the five olfactory organs described in mammals have been described in the pig. **Figure 5**. Shows the five olfactory organs described in rats. Of these five organs, only the main olfactory epithelium (MOE) and the vomeronasal organ (VNO) have been described in the pig (**Figure 6**). The Grueneberg ganglion (GG) is the sensory organ that senses alarm pheromones in mice. Scientist believe that pigs may also have alarm pheromones [39], but they have not been isolated, nor has the GG been found in the pig. Little is known about the septal organ (SO) or the chemical sensory cells of the Trigeminal Nerve in the pig (or in other species). We do believe that the MOE receives molecules in an aerosol, while the VNO receives molecules in liquid form. The GG and SO may also need an aerosol because they are in the nasal airway where aerosols pass as the animal breathers or sniffs.

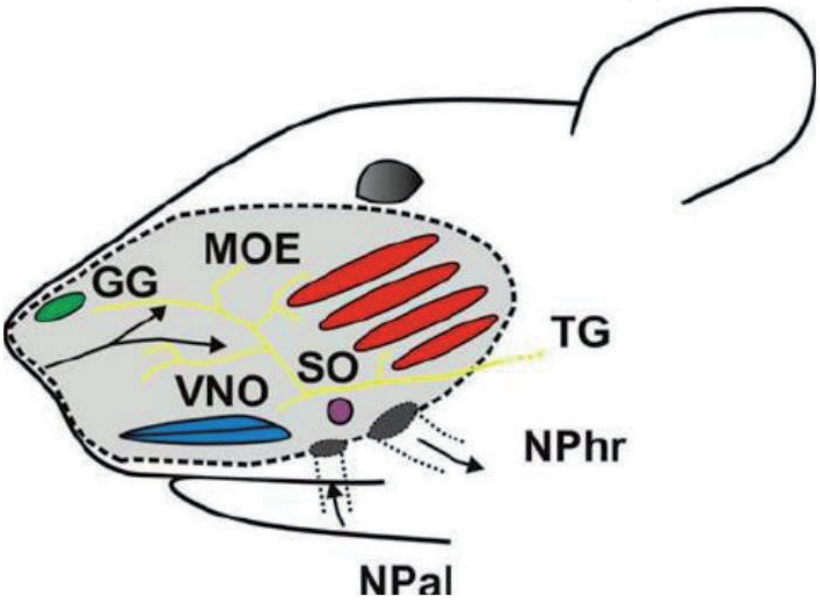

Figure 5.
Chemosensory epithelia in the rat nose. GG, Grueneberg ganglion; MOE, main olfactory epithelium; SO, septal organ of Masera; TG, trigeminal system/nerve; NPal, nasopalatine duct; NPhyr, nasopharyngeal duct. Arrows represent the direction of air flow. From Dauner et al. [37].

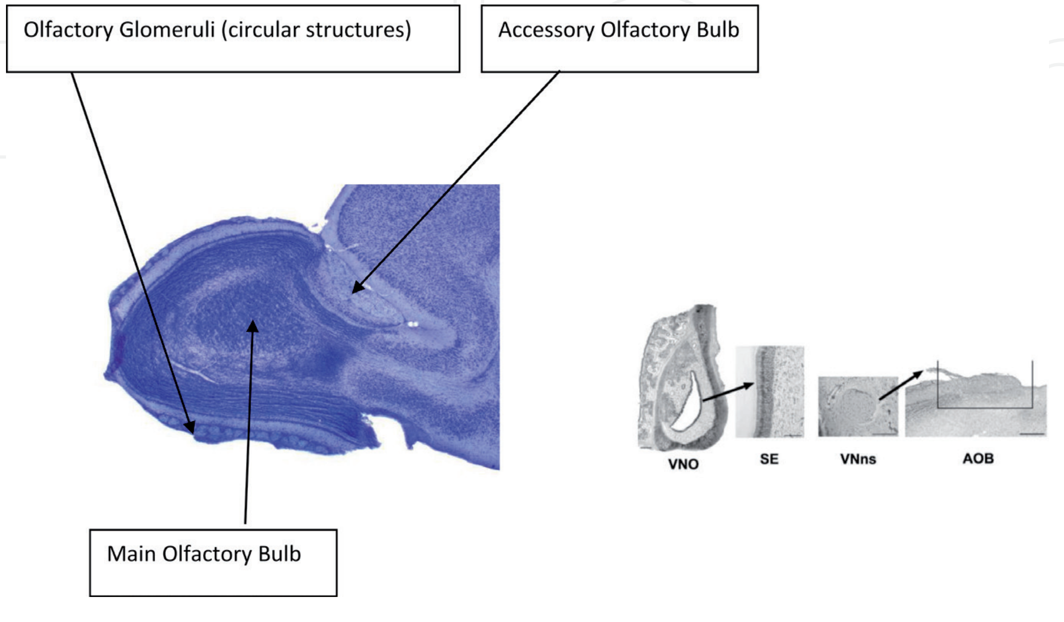

Figure 6.
Ignacio Salazar pictures of the pig VNO (right) and the main olfactory bulb (left) with the AOB shown. VNO pictures are from Salazar et al. [38]; olfactory bulb histology is from Salazar, personal communication.

In addition to the olfactory organs, the nasal mucosa contains several olfactory binding proteins (OBPs). Patricia Nagnan-Le Meillour [40] has done the most recent work in pig's OBPs. When the nasal epithelium receives a chemical signal, that signal can bind an olfactory receptor directly, or more commonly for bioactive chemicals, it binds an OBP and it is the OBP odorant complex that activates the olfactory receptors. It is likely that, before pheromone exposure, a small amount of OBPs are present in the olfactory epithelium mucosa. Pheromone exposure increases OBPs synthesis. Thus, we speculate that a second pheromone exposure 30–60 min after the first exposure could have a large effect on olfactory perception because more OBPs will be present to carry the odorants to the olfactory receptors. However, this still needs to be experimentally demonstrated.

In **Figure 6**, we show excellent anatomical histological pictures of the pig MOE and the VNO by Salazar [38] (personal communication). He and his laboratory they showed that the MOE and VNO are fully present at birth in piglets.

The VNO is thought to be the olfactory organ in which pheromones are perceived. But we know now that this is not always the case. One of the boar sexual pheromone molecules is sensed by the MOE [41]. The other three molecules may be sensed by the VNO or the MOE or any of the other olfactory organs not yet described in the pig. Our behavioral observations of the sow when she experiences a liquid containing a pheromone show that they chomp (see **Table 1**). We believe this behavior is analog to the flehmen behavior in other animals and that, by doing this, sows expose the VNO as well as the MOE to the pheromone.

The VNO receives chemical signals from liquids. Some mammals (except humans and some primates) show flehmen (lip curl) behavior when they are drawing liquid chemical signals into the VNO. An example is when the bull licks cow urine and draws it into the VNO. It is likely that more than one olfactory organ is needed to sense complex pheromones that are mixtures of molecules (like the boar pheromone). The pig is not well-known to show Flehman, but they may Flehman when they receive a chemical signal in liquid form.

6. Pheromone concepts

The field of sexual behavior and pheromonal modulation of sexual behaviors have unique terminology. **Table 4** provides definitions of key terms used in pheromone biology in its widest sense. This may help the reader navigate this area. The broadest term is Semiochemical in which all chemical communication falls. Sexual pheromones are species specific (the cattle sex pheromone is different than the pig sex pheromone). Certainly, the pig uses chemical communication within and between species, for example, when a pig finds a buried truffle or when a plant drives away insects—these between-species forms of chemical communication are not discussed here. We are mostly concerned with the species-specific boar pheromone that stimulates sow reproductive behavior and performance.

The pheromone concept was first described in insects by Karlson and Luscher in 1959 [42] and at the time, they were primarily referring to insect pheromones. Certainly, semiochemicals are found in most plants and animals. Pheromones were previously referred to as ectohormones. This means a hormone that works outside the animal. But pheromones do not meet the definition of a hormone, although the definitions are similar. Karlson and Luscher [42] used the term pheromone to describe a species-specific molecule that is secreted or excreted

Word	Definition
Pheromone	• Substances that are excreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction, for example, a definite behavior or a developmental process [42] • A chemical substance that is usually produced by an animal and serves especially as a stimulus to other individuals of the same species for one or more behavioral responses [43] • A pheromone is an externally secreted signal that sends meaningful information to members of the same species [44]
Kairomone	• A chemical substance emitted by one species and especially an insect or plant that has an adaptive benefit (such as a stimulus for oviposition) to another species [45] • Kairomones are ligands emitted from one species that generate behavior in another species (such as aversion upon detection by a prey species) [45]
Allomone	• A chemical substance secreted externally by certain animals affecting the behavior or physiology of another species detrimentally [46] • A chemical that is released by one species that influences the behavior or physiology of a different species. The organism releasing the substance usually benefits. Allomones are a type of semiochemical used in warning [47]
Synomone	• An interspecific semiochemical that is beneficial to both interacting organisms [48]
Interomone	• An interomone is defined as a semiochemical that acts as pheromone of one species but elicits physiological responses in a different species where the pheromone molecules have not yet been identified [49]
Semiochemical	• A chemical substance or mixture released by an organism that affects the behaviors of other individuals (could be between or within species) [50]

Table 4.
Definitions of common words in mammalian olfactory communication.

from one animal that changes the physiology or behavior of another animal of the same species. The concept was adopted rapidly among invertebrate and vertebrate animal scientists.

Most of the work on mammalian pheromones has been done with rodents. The pig has a highly developed olfactory system (see above), but little work has been done recently on pig pheromones including sexual pheromones. We can learn from work on other species so that we can predict possible pheromones and pheromone effects in the highly-olfactory domestic pig.

An early concept was the bifurcation between priming and releasing pheromones. This dichotomy will be familiar to people who work in pig breeding with gilts and sows. The gilt develops from pre-puberty to post-puberty at around 120–200 days of age. A pheromone that stimulates the onset of puberty, for example, would be a priming pheromone. Boars certainly cause gilts to have an earlier onset of puberty (see Boar effect above). The molecule(s) that are responsible for priming gilts have not been described, but are likely to be the same as the boar pheromone. Most people might believe at this time that the boar sexual pheromone that causes sexual behavior and stimulates gilt puberty are likely to be the same molecules.

A releasing pheromone is one or more molecules that cause a rapid onset of behavior; sexual behavior in this case. Another releasing pheromone might be one that causes pigs to eat, or piglets to nurse, or pigs to fight, or pigs to stop fighting [39, 51]. None of these releasing pheromone molecule(s), other than the boar pheromone have been described.

What can we learn from other mammalian sexual pheromones? Given that the pig has so many functional receptors, it is likely that if a type of pheromone was described in another mammal that the pig would have a pheromone with a similar effect. Here we summarize the classic reproductive pheromones. Note that each early reproductive pheromone was named after the scientist who first reported the effect.

6.1 The Bruce effect

Hilda Bruce described what has been called the Bruce effect in 1959 [52]—before the concept of pheromone was established. She showed that when a pregnant mouse was exposed to an adult male, preferably a dominant male, that the pregnant mouse lost her pregnancy. The Bruce effect has been replicated by many investigators and what we know is that each male has a specific major histocompability complex (MHC) class 1 protein that is secreted in its urine. The father of the mouse litter has a given MHC protein. If a new male enters the cage with a different MHC protein, the female is likely to lose her pregnancy (not 100% of the time, but at a significant rate). The male MHC protein binds the VNO in the female mice. It makes one wonder if heat checking with a boar during pregnancy might contribute to a lower farrowing rate.

The Bruce effect has not been clearly documented in the pig. Assuming the Bruce effect is found in pigs, one would change the management of the sow herd. On most farms, pregnant sows experience a live, often dominant, boar walking the aisle to see if any bred sows are now in heat (meaning their pregnancy has failed). That live boar would not have the same MHC as the father of the litter because they are commonly bred by artificial insemination. We know that a small (5–10%) percentage of sows lose their pregnancy from breeding until farrowing. Part of this effect could be due to the Bruce effect. To manage this situation, pregnant sows should never experience a live boar that is not the father of her litter or perhaps is not the boar present during breeding. Keeping in mind that the Bruce effect is mediated by MHC proteins and not the boar pheromone, one can use the boar pheromone to check for return to estrus in pregnant sows without inducing the Bruce effect.

6.2 The Vandenbergh effect

John Vandenbergh first described this pheromone in a paper published in 1975 [53]. He showed that female mice have an accelerated onset of puberty when exposed to an adult male mouse or urine from an adult male mouse. The molecule was thought to be a protein, but the actual molecule had not been described.

Pigs clearly show the Vandenberg effect. Gilts will have a delayed onset of puberty if they do not experience an adult boar. With boar exposure, the onset of puberty is accelerated in gilts [54]. The pheromone molecule(s) that are responsible have not been described. One might predict that the boar pheromone that stimulates sow reproductive behavior and performance [5], is the same pheromone that stimulates the accelerated onset of puberty in gilts. However, if these boar pheromone molecules are responsible for the Vandenberg effect in gilts, then the dose and number of applications required to cause the Effect have not yet been determined.

6.3 The Whitten effect

Whitten described the Whitten Effect in a number of papers from 1956, 1957 and 1966 and 1968 [55–58]. The Whitten Effect states that in a group of post-pubertal females, the presence of either other cycling adult males will cause the females to synchronize their estrus (or menstrual) cycles. Likewise, adult females tend to synchronize their cycles over time when they are housed together. The Whitten Effect has no valuable application in modern pork production at this time that we can think of; however, production systems change over time and there could be an application in the future. The Whitten Effect takes weeks or months to have its effect. Therefore, we do believe that when gilts approaching puberty are exposed to a boar, that the number or percentage that come into estrus is not evenly distributed over the 21-day cycle, so this may be happening. Boar exposure may partially synchronize a group of gilts first estrus.

7. Benefits to not using a live boar

7.1 General benefits

Boars are found on most modern pig farms. They are needed to find sows in estrus when AI is used. Below are reasons to not have boars on the farm. The reasons include cost, safety and disease control.

The boar costs money to buy and they cost money to maintain. Besides the direct cost of the boar, the boar does not live a good life. They are heat checking sows often and rarely if ever breed. They are often housed in a crate or stall individually for their own safety and the safety of other sows and boars.

Boars are dangerous to have on farms. One large farm in the USA reported that they budget $500,000 per year for boar-induced human injuries. The boar can take a single swipe at a person and damage the person severely. If a boar was very aggressive, they could do great damage to a person. While rare, boars sometimes step on people, or bite people or knock them down if a person stands in the way of the boar and his intended direction.

Boars carry disease. While sows move from breeding to gestation to farrowing and back to breeding, the boar resides in the barn for a long time (a year or more). The boar can be a reservoir of disease and continually infect new breeding sows.

When a serious disease (foot and mouth, ASF, etc.) is found in a country, they often limit movement of adults in some or all regions. If the farm cannot get live adult boars, and have no access to pheromones, the breeding rates will be very low.

7.2 Pheromone applications in the field

7.2.1 Sows

Melrose [35] first suggested Androstenone was the boar pheromone. But we and others have observed that this single molecule was not sufficient to elicit the full sexual behavioral response in estrus sows. This led to the project to seek and discover the complete boar pheromone. This was accomplished by using advanced GC-MS technology to identify three unique molecules that are found in boar saliva and not found in sow saliva [59]. If one examines **Figure 4**, is clear that androstenone alone has only a small effect on sows expressing estrus when they are in fact in heat. But the three molecules together give the largest increase in sow sexual

Parities	Total born/litter	Born alive/litter
1–3	0.88*	0.73*
4–6	−0.10	−0.23
Overall	0.40*	0.22*

*Difference in measures. LSMEANS within a row that differ (P < 0.01) have an *.*

Table 5.
Results from McGlone et al. showing that BOARBETTER® caused an increase in pigs born and born alive in parities 1–3 on 12 farms.

behavior. Furthermore, data we collected recently showed that most sows identified in estrus by a boar, also express estrus behavior to the three-molecule pheromone called BOARBETTER® (BB).

Boar Better (BB) was formulated to include all three molecules in an analog to the natural pheromone. When BB was applied to 12 USA farms in different USA states on nearly 4000 sows, it was discovered that BB increased Farrowing Rate, and litter size born (total or alive). Together, the increase per batch of pigs was significant—over 8% more pigs born per batch. The effect on early parities (1–3) was greater than for older sows that may have maximized their uterine capacity (**Table 5**). Note that while the overall increase in total pig born per litter was 0.40 more pigs with BB, in parities 1–3, the increase was 0.88 pigs/litter due to BB. This is a remarkable improvement in reproduction that cannot be achieved by any common animal health product on the market.

7.2.2 Gilts

While we believe and hope that BB is also the priming pheromone that accelerated gilt puberty, we do not have solid data to show that this is the case. These studies are underway now. We know cycling gilts can be bred with BB because it is a powerful releasing pheromone. Still, because the live boar can stimulate the onset of puberty, it is likely that BB is also the priming pheromone.

8. Future research needs on farms

This area of research is ripe for new discoveries. We know that the pig has a highly developed sense of smell. And we know that pheromones are a major player in the modulation of sexual and other behaviors. The sow releasing pheromone has been discovered and it contains three boar-unique molecules. The primer pheromone that brings gilts into heat has not been identified. It seems likely that the priming pheromone is the same set of molecules that comprise the releasing pheromone. But this must be confirmed through experimentation and practical applications.

We also demonstrate that the novel boar pheromone that was recently discovered induces both sexual behavior in estrus sows and it increases the change of reproductive success in sows. This pheromone is the only known molecule to cause the full effect in behavior and reproduction.

We do not know anything about three olfactory organs that are described in mice, but not yet described in the pig (SO, GG, Trigeminal nerve). Locating these in the pig and documenting how they modulate behavior will be important in the future.

9. Conclusions

This chapter was written to first give the reader a background on boar and sow reproduction, olfaction and pheromones. If one wants to delve deeper in this subject, understanding the biology of the pig is helpful.

Measures of reproductive success on commercial farms show that swine reproduction can be improved on commercial farms by use of a synthetic analog of the natural boar pheromone. Breeding rates should be more successful with the full understanding of the sow's behavior before, during and after her estrous cycle both in housing facilities and free roaming herds. As well as, the different stages of estrous to properly recognize the different measurements for signs of a sow in estrus. The anatomy of the animal also plays a critical role for the pheromones to initiate her "standing reflex" through the different olfactory organs, which help determine if she is in estrus or not. The key point of this is remembering to look for the signs that are visible to show that the sow may be in heat; unreliable indicators are pricked ears, low, deep grunts, vulva temperature and color. The most important sign of estrus is when the sow shows, the standing reflex or locked up behavior. Locked up is the only behavior that indicates estrus in all sows (except those anestrus). Ultimately, the ability to properly detect sows in heat with or without a boar will save time, labor and money. With the assistance of the product BB (which contains three molecules: Androstenone, Androstanol, and Quinoline), stockpeople may be able to attain improved reproductive performance.

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Conflict of interest

Only the first author (JJM) declares a conflict of interest. He is the inventor on the patent on Boar Better which Texas Tech University has licensed to Animal Biotech (of which he is a minority owner). All other authors do not declare any conflict of interest.

Author details

John J. McGlone*, Edgar O. Aviles-Rosa, Courtney Archer, Meyer M. Wilson, Karlee D. Jones, Elaina M. Matthews, Amanda A. Gonzalez and Erica Reyes
Laboratory of Animal Behavior, Physiology and Welfare, Texas Tech University, Lubbock, TX, USA

*Address all correspondence to: john.mcglone@ttu.edu

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