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Responsiveness to boar stimuli and change in vulvar reddening in relation to ovulation in weaned sows¹

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ABSTRACT: In 117 weaned sows, changes in estrous behavior and vulvar reddening were related to timing of ovulation. Detection of estrus was performed every 8 h with four levels of boar stimuli to record the change in responsiveness to these stimuli. This resulted in four overlapping phases of estrus, during which a standing response could be evoked: 1) man estrus (standing response to a back pressure test, in the absence of a boar), 2) spontaneous estrus (standing response in the presence of a boar, no back pressure test), 3) boar estrus (standing response to boar + back pressure test), and 4) detection-mating-area estrus (back pressure test in the presence of four boars). In addition to the detection of estrus, the change in reddening of the inner vulvar mucosa was recorded. Manifestation of estrus in response to the four stimuli occurred in 46, 56, 90, and 97% of the sows, respectively. Onset of the four phases occurred 24 h (SD 13 h), 23 h (SD 15 h), 34 h (SD 13 h), and 41 h (SD 12 h) before ovulation. The duration of the intervals between the various phases of estrus explained 10 to 50% of the variation in the timing of

ovulation relative to the onset of the phases. However, these intervals could not be calculated for all sows because estrus was not expressed at every stimulus level by each sow. The end of vulvar reddening occurred, on average, 21 h (SD 14 h) before ovulation. Except for five sows that ceased to show vulvar reddening within 5 h after ovulation, the end of vulvar reddening occurred before ovulation, within a 70-h range. Of the sows showing boar estrus, 90% also showed vulvar reddening. For sows that showed vulvar reddening until after the onset of boar estrus (two-thirds of the sows), the end of reddening occurred within a much smaller range: from 36 h before, until 2 h after, ovulation. Onset of estrus, regardless at which stimulus level it is detected, appears too variable relative to timing of ovulation to be used as a predictor for ovulation. Duration of the different stages of responsiveness explains only some of this variation and cannot be obtained on all sows. Combining information on vulvar reddening and boar estrus can predict ovulation within a reasonable range for two-thirds of the sows.

Key Words: Boars, Estrus, Ovulation, Sows

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Introduction

In sows, optimal results in terms of fertilized oocytes are achieved when artificial insemination takes place in the period of 24 h before ovulation (Soede et al., 1995). Prediction of ovulation is therefore a necessity in AI strategies focused on maximal fertilization with a low number of inseminations. Onset of estrus is a poor predictor because of the large variation in its timing

relative to ovulation (Soede and Kemp, 1997). Duration of estrus is a fairly good indicator of ovulation, because it takes place approximately two-thirds of the way through the period of behavioral estrus (Nissen et al., 1997). However, duration of estrus cannot be assessed in advance of ovulation.

In the course of estrus, responsiveness to stimuli applied to evoke estrous behavior (standing response) increases and then decreases again. Willemse and Boender (1967) divided the period of estrus into three stages, based on the responsiveness to either a human (referred to as *man estrus*) or a boar (*boar estrus*) as stimuli for detection of estrus. Man estrus covered the middle two-thirds of boar estrus. The authors did not detect ovulation, but insemination results suggested that it took place during the second half of man estrus. Applying additional levels of stimuli during detection of estrus might distinguish more phases of responsiveness and yield a more accurate predictor of ovulation. In addition

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to behavioral characteristics, physical characteristics might yield a predictor of ovulation. Vaginal temperature and conductivity of vaginal mucus are poorly related to the timing of ovulation (Stokhof et al., 1996; Soede et al., 1997). In the current study, changes in behavioral estrus and vulvar reddening were monitored, in order to establish a suitable predictor for ovulation.

Materials and Methods

Animals and Housing

Data on estrus and ovulation in the current study were obtained from an experiment described by Langendijk et al. (2000). The experiment was approved by the Wageningen University ethical commission on animal experiments and was conducted between February and May of 1998. In one group of 10 and in six groups of 20, multiparous sows ($n = 130$) arrived at the experimental farm on the day of weaning, at 2-wk intervals. The sows were obtained from a commercial farm and consisted of a Yorkshire \times Dutch Landrace commercial breed. Litter size averaged 10 and ranged from 7 to 13 piglets; length of lactation was 19 d on average and ranged from 13 to 23 d. At the experimental farm, sows received 2.5 kg of a commercial sow diet (12.9 MJ/kg ME, 130 g/kg CP) in two portions daily (after detection of estrus) and free access to drinking water during 30 min after feeding. Seventy-eight sows were housed individually in crates (2.2×0.65 m), and 52 sows were housed in groups of 4. The group-housed sows had access to 2.6 m² per sow, plus four individual crates in which they were locked up during detection of estrus and feeding. The four boars that were used for detection of estrus were housed in the same barn as the sows. These were commercial AI boars (Dalland, Merselo, The Netherlands), 11 mo of age at the start of the experiment. The boar pens were situated at a distance of at least 4 m from the sows and were separated from the sows by a nontransparent screen that reduced visual, auditory, and olfactory contact.

Detection of Estrus and Boar Stimuli

Sows were checked for estrus daily at 0800, 1600, and 2400 from 57 h until 8 d after weaning. Before detection of estrus started, reddening of the deep inner vaginal mucosa was judged in all sows by spreading the vulvar lips. Both detection of estrus and judging of vulvar reddening were performed by one of two experienced persons, according to a precisely defined protocol. Reddening was scored as 0 (pale), 1 (pink), 2 (red), or 3 (dark red). The onset of vulvar reddening was defined as 4 h before the first time a score of minimal 2 was given, and the end of vulvar reddening was defined as 4 h after the last time a score of minimal 2 was given. Every time detection of estrus was conducted, sows were checked for a standing response in reaction to a

set of increasing levels of boar stimuli. First, all sows were checked for a standing response in absence of a boar using the back pressure test (**BPT**). A back pressure test lasted approximately 20 s and consisted of mimicking the tactile stimuli of the boar by pushing the sow in the flanks and rubbing and pressing the sows' back. If the sow reacted with a frozen stance, arched back, and cocked ears, this was recorded as a standing response. Second, approximately 15 min after the BPT, one of the four teaser boars (randomly chosen) was led in front of the crates and group pens. The teaser boar was restricted to four sows at a time and the sows were observed for a spontaneous standing response (within 30 s). Third, the BPT was performed on each sow, in the presence of the teaser boar, immediately after having observed for the spontaneous standing response. Finally, a fourth stimulus level was applied to 104 of the 130 sows, approximately 25 min after the third stimulus level. These sows were led into a detection mating area (**DMA**) in fixed groups of four. The DMA is an area of 4.5×4.8 m surrounded by four boar pens, designed to maximize boar stimuli during detection of estrus (Hemsworth, 1991). In the DMA, sows have visual, auditory, olfactory, and head-to-head contact with the boars, and can interact with each other. After 5 min in the DMA, the sows were checked for a standing response by a BPT. To check whether the extra boar stimulation in the DMA affected estrous expression, 26 sows received only the first three levels of stimuli during detection of estrus. On the day of arrival (d 0) and on d 1, the 104 sows that were also submitted to the fourth stimulus (DMA) were allowed into the DMA for 15 min, to adapt to the procedure.

Depending on the stimulus level used to evoke a standing response, four overlapping phases of estrus could be defined (Figure 1). These phases were defined as man estrus, spontaneous estrus, boar estrus, and DMA estrus for the four levels of stimuli, respectively, as described above. The onset of a phase was defined as 4 h before the first detection of the standing response, and the end of a phase was defined as 4 h after the last detection of a standing response. Onset of the different phases are denoted T1, T2, T3, and T4 (Figure 1). The interval between the onset of DMA estrus and the onset of boar estrus (T1 to T2), was defined **Int**_{DMA-boar}. The intervals between the other phases were calculated similarly: **Int**_{DMA-man} (T1 to T4), **Int**_{DMA-spont} (T1 to T3), **Int**_{boar-man} (T2 to T4), **Int**_{boar-spont} (T2 to T3), and **Int**_{spont-man} (T3 to T4).

Ultrasonography

Ovarian condition was checked by transrectal ultrasonography, using a 7.5-Mhz annular array sector probe (Pie Medical, Maastricht, The Netherlands). The method of ultrasonography was developed at our laboratory (Soede et al., 1992) and operated by trained and experienced staff. Ultrasonography was performed on d 3 (d 0 = day of weaning) to detect lactational estrus

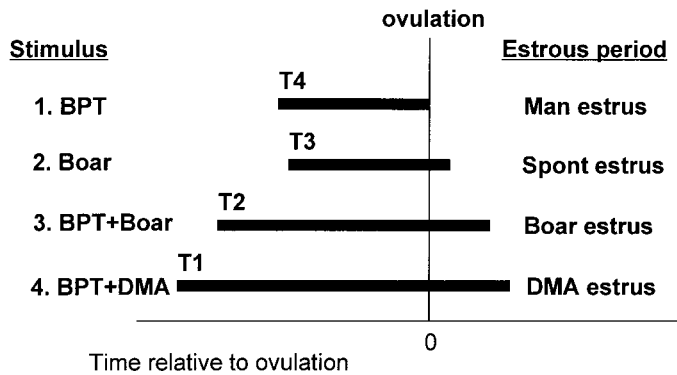


Figure 1. The four subsequent stimuli used for detection of estrus in the experiment (BPT, Boar, BPT+Boar, and BPT+DMA), and the four phases of estrus during which sows responded to these stimuli with a standing response (man estrus, spontaneous estrus, boar estrus, and DMA estrus). BPT: back pressure test. Boar: presence of a teaser boar. DMA: detection mating area, presence of four boars. Intervals between estrous phases were defined $Int_{DMA-Boar}$ (T1 to T2), $Int_{DMA-man}$ (T1 to T4), $Int_{DMA-spont}$ (T1 to T3), $Int_{boar-man}$ (T2 to T4), $Int_{boar-spont}$ (T2 to T3), and $Int_{spont-man}$ (T3 to T4).

(corpora lutea on the ovary) and on d 8 to detect cystic ovaries (follicles > 10 mm), inactive ovaries (no follicles > 4 mm), or silent estrus (ovulation without signs of estrus). From d 3 onward, ultrasonography was performed every 4 h in sows showing estrus in order to record the timing of ovulation. Time of ovulation was defined as the time between the last time preovulatory follicles were detected and the first time no follicles could be detected on the ovary. At the first time when follicles could not be detected on the ovary, diagnosis was always double-checked by a second person. Detection of estrus, ultrasonography, and feeding took approximately 2 h.

Characteristics of Estrus and Statistics

The timing of ovulation was expressed in hours from an estrous characteristic, such as onset of a phase of estrus, or end of vulvar reddening. Timing of ovulation relative to onset of man estrus, spontaneous estrus, boar estrus, DMA estrus, and onset of vulvar reddening was normally distributed (not shown). The variation in timing of ovulation relative to the different characteristics was therefore expressed by the SD of the uncorrected means. To test the hypothesis that length of the intervals between phases of estrus was related to the time from onset of a phase to ovulation, SD (mean square error) was also calculated after correcting for length of the intervals: $Y_{ij} = \mu + \beta_1 \cdot Int_i + e_{ij}$ (Y_{ij} is ovulation in hours after onset of man, spontaneous, boar, or DMA estrus; Int_i is length of an interval between two phases of estrus).

The GLM procedure of SAS (SAS Inst. Inc., Cary, NC) was used to analyze the model. For some sows,

housing (group-housed sows), and detection of estrus in the DMA (52 group-housed sows and 52 individually housed sows), was in groups of four sows. Nevertheless, data on estrus were analyzed for each sow individually because the aim of the study was to estimate timing of ovulation, given the variation caused by different factors, such as group effects. Exclusion of group effects was justified by preliminary analyses, which showed that there was no effect of groups on any of the analyzed characteristics. The housing conditions and the extra boar contact received by the sows that went through the DMA procedure did not affect any of the data studied in this paper (Langendijk et al., 2000). Therefore, these were not included in the model. Interval from weaning to estrus was related to duration of estrus ($P < 0.05$) but did not affect the relation between the timing of ovulation and the length of Int_i for any of the phases. Therefore, the interval from weaning to estrus was excluded from the model. Because most animals showed both boar estrus and vulvar reddening, these two characteristics were combined to predict timing of ovulation. Three categories of sows were defined: sows that showed no vulvar reddening until after the onset of boar estrus, sows that showed vulvar reddening at the onset of boar estrus, and sows that had ceased to show vulvar reddening before the onset of boar estrus. Timing of ovulation in these categories was expressed in hours after the onset of boar estrus and in hours after the end of vulvar reddening. Differences in standard deviation between different estimations of ovulation were tested with the F -statistic. Normality of parameters was tested in the UNIVARIATE procedure of SAS, with the Shapiro-Wilk statistic. Correlations between variables were calculated according to Pearson using the CORR procedure of SAS.

Results

Onset of Estrus in Relation to Ovulation

Of the 130 sows used in the experiment, four sows had ovulated during lactation, seven sows had developed cystic ovaries by d 8, and two sows became too crippled to complete the experimental period. These sows were excluded from further analyses, leaving 117 sows that ovulated. Of these 117 sows, 95 sows had been submitted to four stimulus levels, and 22 sows had been submitted to three stimulus levels. Of the 117 sows, 1 sow did not show standing estrus at any of the stimulus levels, and 2 sows already showed estrus at the first time detection of estrus was conducted. For these three sows, time of ovulation could only be related to vulvar reddening. The number of sows detected in estrus differed between stimulus levels. Of the 117 sows with ovulation, 46, 56, and 90% showed man, spontaneous, or boar estrus; of the 95 sows that were submitted to the DMA stimulus level, 97% showed DMA estrus. On average, the duration of man, spontaneous, boar, and DMA estrus was 24 h (SD 13 h), 27 h (SD 17 h), 44 h (SD 20 h), and 55 h (SD 18 h), respectively.

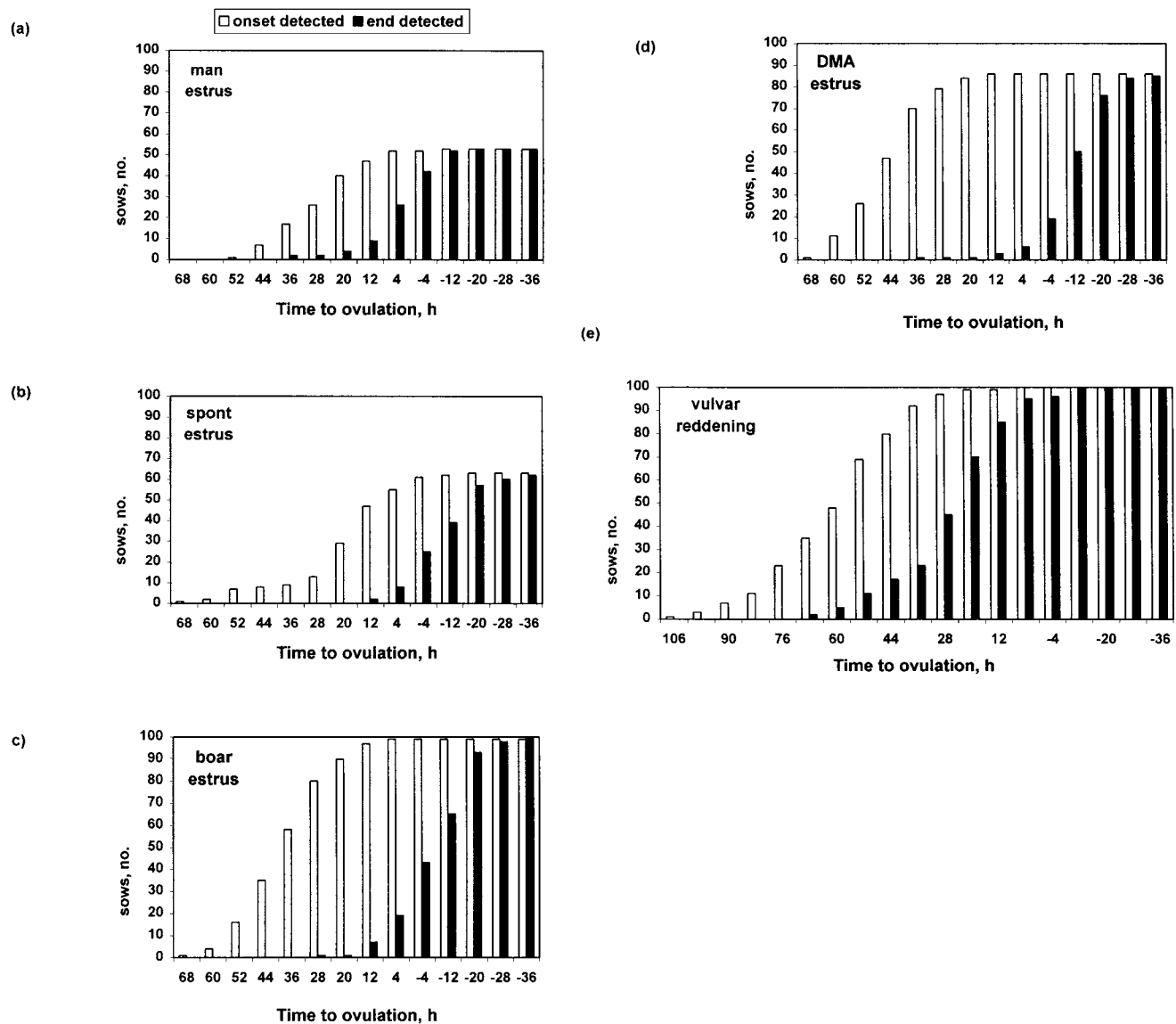


Figure 2. Cumulative number of sows in which onset of standing estrus (open bar) and end of standing estrus (solid bar) was recorded for man estrus (a), spontaneous estrus (b), boar estrus (c) and DMA estrus (d), relative to the timing of ovulation. Man estrus, spontaneous estrus, boar estrus, and DMA estrus were the phases of estrus during which sows showed a standing response to a back pressure test, presence of a boar, back pressure test in presence of a boar, or back pressure test in presence of four boars, respectively. Panel (e): cumulative number of sows in which onset of vulvar reddening (open bar) and end of vulvar reddening (solid bar) was recorded, relative to the timing of ovulation. Vulvar reddening was scored as the reddening of the internal vulvar mucosa.

Onset of behavioral estrus occurred before ovulation at all of the stimulus levels (Figure 2), except for one sow that ovulated before onset of man estrus and two sows that ovulated before onset of spontaneous estrus. Onset of DMA estrus was recorded at 41 h (SD = 12 h) before ovulation on average and followed by boar estrus (34 h; SD = 13 h), man estrus (24 h; SD = 13 h), and spontaneous estrus (23 h; SD = 15 h). On average, intervals from the onset of man estrus to ovulation and from spontaneous estrus to ovulation were similar. Within each stimulus level, the onset of estrus relative to ovulation was very variable between sows. The range between the first and the last sow ovulating after onset

of one of the phases of estrus was between 48 h (man estrus) and 64 h (boar estrus) (Figure 2).

Reddening of the inner vulva, as a sign of proestrus, started 52 h (SD = 18 h) before ovulation and was shown by 87% of the sows. Except for five sows that still had reddened vulvar mucosa until 5 h after ovulation, a score of red was never observed after ovulation (Figure 3). The end of vulvar reddening occurred 21 h (SD = 14 h) before ovulation, but this timing was also very variable. The interval from the end of vulvar reddening to ovulation was not normally distributed ($P < 0.01$), but skewed. The variation in timing of ovulation relative to the end of vulvar reddening was smaller ($P < 0.05$) for

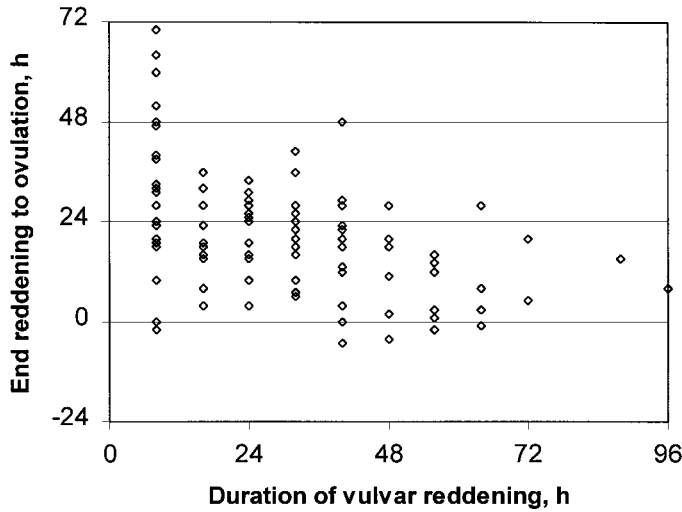


Figure 3. Timing of ovulation in hours from the end of vulvar reddening, in relation to the duration of vulvar reddening. Vulvar reddening was scored by opening the vulvar lips and observing the inner vulvar mucosa.

sows that showed a reddened vulva for a longer period of time (Figure 3); SD was 9.5 h in sows that had a reddened vulva for more than 40 h, compared with a SD of 14 h in sows that had a reddened vulva for 40 h or less. The duration of vulvar reddening was 36 h in sows that ovulated, ranging from 0 to 96 h.

Intervals between Phases of Estrus in Relation to Timing of Ovulation

There was large variation in the length of the intervals between different phases of estrus (SD 11 h to 20 h, Table 1). Onset of DMA estrus preceded or coincided with the onset of boar estrus for 68 of 76 sows, preceded or coincided with onset of spontaneous estrus for 46 of 47 sows, and preceded or coincided with onset of man estrus for 33 of 36 sows. Onset of boar estrus preceded the onset of spontaneous estrus in all sows and man estrus in 45 out of 49 sows. However, in 15 out of 33

sows, onset of spontaneous estrus occurred after onset of man estrus.

For all phases of estrus, the timing of ovulation after onset of estrus was related to length of the intervals between the phases (Table 2). The length of the different intervals explained 10 to 50% of the variation in the estimated timing of ovulation. A 24-h change in the length of an interval was related to a 7- to 19-h change ($P < 0.01$) in the estimated timing of ovulation. Depending on the interval regarded, the timing of ovulation relative to onset of estrus was related either positively or negatively to the length of the interval. The SD of the timing of ovulation was not significantly lower than when the timing of ovulation was related to the onset of estrus only (Table 2).

Combination of Boar Estrus and Vulvar Reddening to Predict Ovulation

Of all sows that ovulated, 87% showed vulvar reddening and 90% showed boar estrus. Therefore, these characteristics were combined in order to determine whether the prediction of ovulation could be improved. At onset of boar estrus, three categories of sows were defined on the basis of vulvar reddening (Table 3): sows that ceased to show vulvar reddening before onset of boar estrus (31% of sows with both boar estrus and vulvar reddening), sows that did not show vulvar reddening until after the onset of boar estrus (13%), and sows with a score of red at the onset of boar estrus (56%). The latter two categories of sows showed less variation in the timing of ovulation as expressed in hours after end of vulvar reddening compared with other sows. Ovulation took place within 36 h after and 2 h before the end of vulvar reddening in these sows. In contrast, sows that ceased to show reddening before onset of estrus ovulated within a range twice as large (70 h after, to 5 h before, the end of vulvar reddening).

Discussion

This study is the first to relate various phases of behavioral estrus, monitored by applying different lev-

Table 1. Mean duration (h) of the intervals between onset of different phases of estrus.

A phase of estrus was defined as the period during which a standing response was exhibited to either a back pressure test (man estrus), presence of a boar (spont estrus), back pressure test (BPT) in presence of a boar (boar estrus), or BPT in presence of four boars (DMA estrus)

Interval ¹	n	Mean, h	SD, h	Minimum	Maximum
Int _{spont-man}	33	1	20	-40	48
Int _{boar-man}	49	11	17	-40	56
Int _{DMA-man}	36	21	17	-8	56
Int _{boar-spont}	59	15	11	0	40
Int _{DMA-spont}	49	19	13	-8	48
Int _{DMA-boar}	78	8	11	-16	32

¹Int_{spont-man} is the interval between onset of spont-estrus and onset of man-estrus; Int_{boar-man} is the interval between onset of boar-estrus and onset of man-estrus, and so on.

Table 2. Variation (SD) in time between onset of an estrous phase and ovulation, before and after correction for the length of intervals between different estrous phases. A phase of estrus was defined as the period during which a standing response was exhibited to either a back pressure test (man estrus), presence of a boar (spont estrus), back pressure test (BPT) in presence of a boar (boar estrus), or BPT in presence of four boars (DMA estrus)

Ovulation, hours from	Related to duration of	n	Mean, h	SD1 ^a	SD2 ^b	β^b	R ²
Onset of man estrus	Int _{DMA-man}	36	23	15	10	-0.6*	0.5
	Int _{Boar-man}	49	25	13	9	-0.5*	0.5
	Int _{Spont-man}	33	25	15	13	-0.4*	0.3
Onset of spontaneous estrus	Int _{Spont-man}	33	26	17	13	0.6*	0.5
	Int _{Boar-spont}	59	23	15	12	-0.8*	0.3
	Int _{DMA-spont}	47	24	14	10	-0.7*	0.4
Onset of boar estrus	Int _{DMA-boar}	76	35	13	10	-0.7*	0.4
	Int _{Boar-man}	49	36	13	9	0.5*	0.4
	Int _{Boar-spont}	59	38	13	13	0.2	0
Onset of DMA estrus	Int _{DMA-boar}	76	42	11	10	0.3*	0.1
	Int _{DMA-man}	36	44	12	10	0.4*	0.3
	Int _{DMA-spont}	47	43	11	10	0.3*	0.1

^aSD1: Standard deviation of the uncorrected means, calculated for the sows in which the length of the concerning interval could be calculated. SD2: Standard deviation for the same sows (mean square error), after correction for the length of the concerning interval (see model below).

^bThe terms β and R² calculated from the model: $Y_{ij} = \mu + \beta \cdot \text{Int}_i + e_j$, with $Y_{ij} = h$ to ovulation and $\beta =$ regression coefficient for length of interval Int_i .

* $P < 0.05$.

els of stimuli during detection of estrus, to the timing of ovulation. The responsiveness to boar stimuli, used for the detection of estrus, increased in the period before ovulation. As a consequence, onset of DMA estrus occurred earliest, relative to ovulation, and was followed by boar estrus. Onset of man estrus and spontaneous estrus did not occur in the same order in all sows. Apparently, the presence of a teaser boar (without BPT) and the back pressure test in absence of a boar are perceived as different by individual sows with respect to their potential to evoke a standing response.

To satisfactorily predict ovulation for the majority of sows, the predicted timing of ovulation should be within a 24-h range, which is the duration of the period of optimal fertilization (Soede et al., 1995). To achieve such a prediction with 90% of the sows within this 24-h range, the standard deviation of the predicted timing of ovulation must not exceed 7.5 h. Moreover, a predictor of ovulation is only suitable if it can be obtained in the majority of sows. Onset of estrus did not yield a prediction of ovulation with a standard deviation of less than 7.5 h at any of the stimulus levels used in this

Table 3. Onset of boar estrus^a and end of vulvar reddening^b in hours to ovulation, depending on the manifestation of vulvar reddening as related to the onset of boar estrus

Time of ovulation, h	Category of sows	Time of ovulation, h				
		n	Mean, h	SD, h	Minimum	Maximum
	All sows showing boar estrus	99	34	13	0	64
From onset of boar estrus	Vulvar reddening ceased before onset of boar estrus	28	26	14	4	64
	Vulvar reddening at onset of boar estrus	51	38	10	18	60
	No vulvar reddening until after onset of boar estrus	20	38	11	14	56
From end of vulvar reddening	Vulvar reddening ceased before onset of boar estrus	28	30	19	-5	70
	Vulvar reddening at onset of boar estrus	51	18	10	-2	36
	No vulvar reddening until after onset of boar estrus	12	16	10	-1	33

^aBoar estrus: phase of estrus during which standing response was shown to a back pressure test in presence of a teaser boar.

^bEnd of vulvar reddening: 4 h after the last time inner vulvar mucosa was judged as being red.

study. The least variation was found in the timing of ovulation relative to onset of DMA estrus (SD = 12 h). The range between the first sow and the last sow ovulating after onset of estrus was between 48 h (man estrus) and 64 h (boar estrus). Several studies reviewed by Soede and Kemp (1997) have shown the huge variation in the timing of ovulation after onset of boar estrus. In those studies, ovulation occurred 35 to 45 h after onset of estrus on average, and the range in the timing of ovulation increased up to 70 h within a study. From the current study, it appears that, at other stimulus levels, the range in the timing of ovulation relative to the onset of estrus is also large.

The large variation in timing of ovulation relative to onset of the different phases of estrus was related to the variation in the length of the intervals between phases. The length of these intervals explained 10 to 50% of the variation in the timing of ovulation. Willemse and Boender (1967) suggested that, in gilts, the duration of estrus as detected in the absence of a boar (man estrus) always covers the middle two-thirds of the duration of estrus as detected in presence of a boar (boar estrus) and that ovulation occurs during the second half of man estrus. This would imply that the length of the intervals between phases of estrus is related to the time from onset of a phase to ovulation. From our data, it seems that indeed there is a relation between the length of the intervals and the timing of ovulation. However, length of the intervals never explained more than 50% of the variation in the timing of ovulation, and the standard deviation in the predicted timing of ovulation never became lower than 9 h. Moreover, an increase in length of an interval was not always related to an increase in the interval from the onset of estrus to ovulation. For example, a 1-h increase in the interval from onset of boar estrus to man estrus was related to 0.5-h delay in the timing of ovulation relative to the onset of boar estrus, but a 0.5-h decrease in the interval from onset of man estrus to ovulation. This is contradictory to the findings of Willemse and Boender (1967). The different stages of estrus could not be calculated for many sows because they did not show estrus at all stimulus levels. DMA estrus and boar estrus were recorded in 97 and 90% of the sows, but man estrus and spontaneous estrus were recorded in only 46 and 56% of the sows. The percentage of sows showing man and spontaneous estrus was particularly low in sows that were also submitted to the DMA stimulus (41 and 54% vs 68 and 68% in sows without DMA stimulus). During the days preceding onset of estrus, these sows experienced extra boar contact, probably causing habituation to boar stimuli during detection of estrus later on (Langendijk et al., 2000). Low expression of estrus at a stimulus level reduces the applicability as a predictor of ovulation. In this study, a reasonable amount of variation (40%) in the timing of ovulation relative to the onset of boar estrus could be explained by the interval from onset of DMA estrus to the onset of boar estrus in 76 sows. The difference between our findings and

the concept of Willemse and Boender (1967) might be explained partly by the fact that their studies were with gilts. Besides, in their protocol for detection of estrus, detection was performed without a boar as soon as a standing response could be evoked in absence of a boar. As pointed out before, the high level of boar contact that was maintained throughout estrus in our protocol might have affected the expression of estrus and thereby the relation between duration of various phases of estrus and the timing of ovulation. With a protocol comparable to the current study, Soede et al. (1996) also found a weak relationship between the duration of estrus detected in the absence of the boar and the duration of estrus detected in the presence of the boar ($R^2 = 0.25$). Apparently, recording the increase in responsiveness in the course of estrus by applying different detection stimuli does not substantially improve the prediction of the timing of ovulation.

Relating the timing of ovulation to changes in vulvar reddening yielded the greatest error in the estimated timing of ovulation; ovulation took place from 70 h after, to 5 h before, the end of vulvar reddening. Vulvar reddening and vulvar swelling as a sign of approaching estrus are probably related to the rise in circulating estrogens during the follicular phase, which stimulate blood flow in the genital organs (Rojkittikhun et al., 1992). The density of estrogen receptors in pig uterine and cervical tissue (Stanchev et al., 1984, 1990) and in chimpanzee perineal sex skin (Ozasa and Gould, 1982) increases enormously during the late follicular phase and is highest during estrus. Following the rise of the preovulatory LH surge, plasma estradiol concentrations start to drop and reach basal levels during the day before ovulation (van de Wiel et al., 1981). A concomitant decrease in related vulvar reddening might be expected. In our study, no vulvar reddening was scored after ovulation, except for five sows that ceased to show vulvar reddening within 5 h after ovulation. The end of vulvar reddening took place at 21 h before ovulation. These facts indicate that there is a relationship between the decline in circulating estrogens before ovulation and vulvar reddening, although the end of vulvar reddening ranged from 70 h before, to 5 h after, ovulation. The great range in the interval from the end of vulvar reddening to ovulation was related to the duration of vulvar reddening. In sows with a shorter duration of vulvar reddening, ovulation took place within a 75-h range from the end of reddening. In the sows with a longer duration of vulvar reddening, the range in timing of ovulation relative to the end of vulvar reddening to ovulation was less, approximately 30 h.

Combining information on boar estrus and vulvar reddening gave a more precise estimation of the timing of ovulation. Sows that showed vulvar reddening at or after onset of boar estrus (56 and 13% of the sows that showed boar estrus) ovulated 17 h (SD = 10 h) after the end of vulvar reddening. End of vulvar reddening occurred within a range of 36 h before and 2 h after ovulation. In sows that had already ceased to show

vulvar reddening at onset of estrus this range was twice as large. This means that sows with vulvar reddening at onset of boar estrus, will hardly ever ovulate before the end of vulvar reddening. Insemination in these sows can be postponed until the end of vulvar reddening.

Implications

Onset of estrus as detected at different stimulus levels shows too much variation to be used as a predictor for the timing of ovulation. Recording the increase of responsiveness to boar stimuli used for detection of estrus explains some of this variation, but not enough to accurately predict ovulation. Moreover, not all sows show estrus at every stimulus level. The timing of onset and end of vulvar reddening relative to ovulation are too variable to predict ovulation. Vulvar reddening, however, hardly ever takes place after ovulation and is therefore a sign that ovulation still has to take place. This information can be used to postpone the first insemination in sows that still show vulvar reddening. Besides, sows that show vulvar reddening at or after onset of boar estrus, ovulate within a reasonable range from the end of reddening. Combination of information on vulvar reddening and onset of boar estrus can thus be used to correctly time insemination in about two thirds of sows.

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