<https://helda.helsinki.fi>

The effect of farrowing duration and parity on preovulatory follicular size and oxytocin release of sows at subsequent oestrus

Yun, J.

2018-06

Yun , J , Bjorkman , S , Oliviero , C , Soede , N & Peltoniemi , O 2018 , ' The effect of farrowing duration and parity on preovulatory follicular size and oxytocin release of sows at subsequent oestrus ' , Reproduction in Domestic Animals , vol. 53 , no. 3 , pp. 776-783 . <https://doi.org/10.1111/rda.1>

<http://hdl.handle.net/10138/326481>

<https://doi.org/10.1111/rda.13170>

unspecified

acceptedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

1 The effect of farrowing duration and parity on preovulatory follicular size and oxytocin release of sows
2 at subsequent oestrus

3 - Effects of farrowing duration and parity at subsequent oestrus of sows

4

5 Jinhyeon Yun^{a,*}, Stefan Björkman^{b,*}, Claudio Oliviero^b, Nicoline Soede^c, Olli Peltoniemi^b

6 ^aResearch Centre for Animal Welfare, Department of Production Animal Medicine, P.O. Box 57,
7 00014 University of Helsinki, Finland

8 ^bProduction Animal Hospital, Department of Production Animal Medicine, P.O. Box 66, 00014
9 University of Helsinki, Finland

10 ^cWU Adaptation Physiology Group, Animal Sciences, P.O. Box 338, 6700AH Wageningen, The
11 Netherlands

12 *Joint first and corresponding author. Email: jinhyeon.yun@helsinki.fi; stefan.bjorkman@helsinki.fi

13

14 Contents

15 This study examined the extent to which prolonged farrowing and parity are associated with plasma
16 oxytocin concentrations and follicular development of oestrous sows during subsequent insemination.
17 A total of 30 sows were allocated to two groups based on farrowing duration: 1) SHORT (n = 14): 159
18 $\pm$ 29 min, 2) LONG (n = 16): 533 $\pm$ 190 min. The sows were also divided into two parity classes: 1)
19 YOUNG (n = 14): parity 2.5 $\pm$ 0.8, 2) OLD (n = 16): parity 6.4 $\pm$ 2.3. After weaning, the ovaries were
20 examined daily with transrectal ultrasound. On the second day of oestrus, blood samples were collected
21 for oxytocin (OT) assay at -15, -10, -5, 0, +1, +2, +3, +4, +6, +8, +10, +15, +20, +25, +30, +40, +50

and +60 min with a boar contact between 0 and +10 min. Boar presence stimulated an increase in OT concentrations ($P < 0.05$). During boar presence, OT in the LONG group were higher than in the SHORT group ($P < 0.01$). The sows in the OLD group had a longer farrowing duration than in the YOUNG group ($P < 0.05$). OT levels and diameters of follicles were more relevant for parity than was the duration of farrowing. We therefore conclude that the OT levels and follicular development of oestrous sows are associated due to parity but difficult to be predicted from the duration of previous farrowing.

Key words: sows, farrowing duration, oestrus, boar presence, standing reflex, insemination

1. Introduction

Prolonged farrowing was reported to be unfavourably associated with perinatal mortality (Borges et al., 2005; Fraser et al., 1997; Van Dijk et al., 2005), mainly by increasing the risk of hypoxia in piglets (Herpin et al., 1996). In addition to consequences for piglet vitality, prolonged farrowing also seems to be related to subsequent sow performance. A recent study showed that sows with prolonged farrowing had a reduced pregnancy rate after the subsequent post-weaning insemination (Oliviero et al., 2013). Causes of prolonged farrowing are reported to be large litter size (Borges et al., 2005; Herpin et al., 1996), high parity (Björkman et al., 2017; Oliviero et al., 2010), confined farrowing environment (Gu et al., 2011; Oliviero et al., 2008; Yun et al., 2015), and restricted prepartum maternal behaviour of sows (Pedersen et al., 2006), which are also shown to be associated with a decrease in oxytocin (OT) concentrations during parturition (Björkman et al., 2017; Oliviero et al., 2008, 2010; Yun et al., 2015).

Sufficient myometrial activity is needed during farrowing for rapid expulsion of piglets and consequent prevention of prolonged farrowing (Castrén et al., 1993a; Jarvis et al., 2004; Lawrence et

al., 1997; Oliviero et al., 2008). It is known that OT is one of the major modulators of uterine activity (Higuchi et al., 1985; Taverne et al., 1979). The OT baseline concentrations start to increase about 6 hours before parturition, peak after the birth of each piglet, and decrease thereafter (Castrén et al., 1993b; Gilbert et al., 2002; Oliviero et al., 2008; Yun et al., 2015). Previous evidences consequentially suggested that the reduced basal and peak OT concentrations have been associated with prolonged farrowing (Castrén et al., 1993a; Oliviero et al., 2008).

After weaning, the production and release of OT is stimulated by estradiol produced from follicles (Carter, 1992; Gimpl and Fahrenholz, 2001; Wathes et al., 1996) which is supported by increasing gonadotrophin stimulation, particularly by FSH and LH (Kemp et al., 2005; Van den Brand et al., 2000; Van Leeuwen et al., 2011). The positive relationship between follicular development and estradiol concentrations during the follicular phase was confirmed by several studies (Breuel et al., 1993; Nayudu et al., 1992; Sheldon and Dobson, 2004). However, to the best of our knowledge, there is little research to investigate the association between OT concentrations and follicular size of oestrous sows. OT release is triggered during oestrus by introduction of a boar to the sows (Langendijk, 2003, 2005), and it plays an important role in myometrial activity, and thereby in sperm transportation to the oviducts (Langendijk et al., 2005). Parity also affects myometrial activity at oestrus (Langendijk et al., 2005).

Therefore, the current study aimed to investigate the relationship between previous farrowing duration (FD) and OT levels of the subsequent oestrous sows, and to examine the interactions with size of preovulatory follicles. We also aimed to study the effect of parity on this relationship. We focused on plasma OT concentrations of the oestrous sows, and hypothesized that prolonged farrowing and high parity would be associated with lower OT concentrations of the sows during subsequent oestrus. We also hypothesized that the OT concentrations in oestrous sows would be positively associated with size of preovulatory follicles.

67

68 2. Materials and Methods

69 Experimental procedures were reviewed and approved by the Animal Experiment Board (ELLA:
70 ESAVI/3331/04.10.03/2011) in Finland.

71 2.1. Animals and management

72 Two single experiments were conducted on two different research herds in southern Finland. *Herd 1*:
73 approximately 400 crossbred (Finnish Yorkshire × Landrace) sows were housed in peat-bedded pens (8
74 × 5 m) in groups of 8-10 during pregnancy, and confined in farrowing and lactation pens, which
75 consisted of a conventional steel farrowing crate on a fully-slatted plastic floor during parturition and
76 lactation. *Herd 2*: approximately 280 crossbred (Finnish Yorkshire × Large White) sows were housed
77 in groups, twenty per group pen (20 × 5 m, straw-bedded) during pregnancy, and confined in farrowing
78 and lactation pens which consisted of a conventional steel farrowing crate on a half-slatted concrete
79 floor during parturition and lactation. After a four week lactation period (27.0 ± 1.8 days), all sows
80 included in the study were confined in stalls individually and catheterized two or three days after
81 weaning through the auricular vein following a nonsurgical catheterization procedure (Yun et al.,
82 2017). Starting three days after weaning, standing oestrus of the sow was tested daily at 08:30 and
83 15:30 until detected by applying a back pressure test while the sows had nose-to-nose contact with a
84 boar. For doing that, always the same boar was used in each herd.

85 2.2. Experimental design

86 A total of 30 crossbred sows [19 sows (FD 361.3 ± 210.3 , parity 5.3 ± 3.0) in 4 batches for *Herd 1*,
87 and 11 sows (FD 353.5 ± 284.0 , parity 3.3 ± 1.2) in 3 batches for *Herd 2*] were selected for the study.
88 According to the previous FD, all the sows were allocated to two groups: 1) SHORT: 14 sows (parity

3.8 $\pm$ 2.6) with shorter than 200 min of FD (range 103 – 192 min), and 2) LONG: 16 sows (parity 5.3 $\pm$ 2.5) with FD between 300 and 900 min (range 326 – 878 min). The classification of FD in the present study was set based on the recent studies suggesting that prolonged farrowing was defined as longer than 300 min of FD (Oliviero et al., 2010, 2013). The sows included in the study were also divided into two age classifications: 1) YOUNG: 14 sows with parity between 1 and 3 (average 2.5 $\pm$ 0.8), and 2) OLD: 16 sows with parity between 4 and 11 (average 6.4 $\pm$ 2.3). The parity group was classified based on the previous evidences showing that FD initiated to increase from the 4th parity (Oliviero et al., 2010; Björkman et al., 2017). Sows requiring induced delivery or distinct parturition assistance by farm personnel were excluded from the study.

2.3. Observation of farrowing duration

The farrowings of the sows were video-recorded using internet protocol (IP) cameras (Niceview NICECAN420WL, Niceview Corp.). The cameras were placed behind and 1.5 m above the sows 2 days before expected farrowing date. The sequence output was recorded by IP-camera software (Blue Iris v.2.64, Perspective Software Corp.) and examined with a media player (Windows media player 12.0, Microsoft Corp.) by a trained observer. The display resolution was 640 x 480 pixels, and the frame rate was 2 FPS. FD was determined as time interval between the expulsion of the first and the last piglet.

2.4. Blood collection and oxytocin assay during oestrus

During blood collection, a boar was presented across the stall, and back, flank or both pressures were applied to the sow for 10 min. When initiating sampling, the first 2 ml of blood drawn was discarded, and the sample was taken using single-use vacuum needles into 3 ml EDTA tubes adding 500kIU/ml of aprotinin for *Herd 1* and 4 ml EDTA tubes containing 500kIU/ml of aprotinin for *Herd 2*. Blood

111 samples were collected -15, -10, -5, 0, +1, +2, +3, +4, +6, +8, +10, +15, +20, +25, +30, +40, +50 and
112 +60 minutes from the point of boar introduction. The boar was introduced to the sow for between 0 and
113 10 min.

114 OT concentrations for both trials were measured using an enzyme-linked immunosorbent assay kit
115 (Oxytocin ELISA kit, Enzo Life Sciences, Lausen, Switzerland). Purified plasma samples were
116 reconstituted with 250 µl of assay buffer supplied in the ELISA kit, and analysed in duplicate
117 according to the assay kit instruction. Sensitivities of the plasma OT assays for *Herds 1* and 2 were 7.8
118 pg/ml and 3.9 pg/ml, respectively. Average mass recovery was 89.6% and 90.1%, and the intra- and
119 inter- assay CVs were 4.5% and 9.6%, and 15.1% and 7.4%, for *Herds 1* and 2, respectively.

120 2.5. Measurement of follicle development

121 Transrectal ultrasound examinations (Mylabone vet, 10 MHz, linear array probe, SV3513; Esaote) of
122 the ovaries were performed twice a day at 09:00 and 15:00, starting three days after weaning until
123 ovulation. Both ovaries were scanned at each examination. The clips were exported in DICOM format
124 and analysed using the IMPAX 6.5.5 picture archiving and communication system (Agfa Healthcare,
125 Belgium). The diameters (in mm) of the five largest follicles on the left and right ovary were measured
126 and averaged.

127 2.6. Statistical analyses

128 SAS v.9.4 (SAS Institute Inc., NC, USA, 2012) was used for statistical processing of all data. A
129 nested design using a mixed model was used to compare LS means for FD, litter size, plasma OT
130 concentrations and follicle development between FD class (SHORT and LONG), parity class (YOUNG
131 and OLD) and their interactions. FD and parity classes were nested within the herds. Batch was used as
132 a random effect. The experimental unit was the sow.

133 Repeated measures using a mixed model were used to analyse periodical OT concentrations within
134 four periods relative to the onset of boar presence at 0 min: 1) -15, -10 and -5 min (i.e. before boar
135 presence), 2) 0, 1, 2, 3, 4, 6, 8 and 10 min (i.e. during boar presence), 3) 15, 20, 25, 30, 40, 50 and 60
136 min (i.e. after boar presence), and 4) total period. Interactions between FD and parity classes were
137 analysed with multiple comparisons using the Tukey-Kramer procedure. Post hoc analyses using the
138 Kenward-Rogers procedure were performed to compare the data for OT and follicle development
139 between the treatments in YOUNG or in OLD groups separately. OT concentrations analysed by
140 repeated measures during the total sampling period were used to determine correlations with FD,
141 parity, and diameters of the follicles measured at five days after weaning and when they reached
142 maximum size, using Spearman rank correlation coefficients (r_s). Pearson correlation coefficients (r)
143 were applied to examine correlations of parity with average follicle diameters at five days after
144 weaning and the days it took follicles to reach maximum diameter.

145

146 3. Results

147 3.1. Farrowing duration and litter size

148 Average FD of all sows was 358 (± 235) min, with 159 (± 29) min in SHORT and 533 (± 190) min in
149 LONG groups. The sows in the OLD group had longer FD than those in the YOUNG group (LS means
150 $\pm$ SE: 265 $\pm$ 60 vs. 459 $\pm$ 63 min, $P < 0.05$).

151 The sows in the LONG group tended to have more total piglets born per litter than did those in the
152 SHORT group (14.3 $\pm$ 1.2 vs. 11.5 $\pm$ 1.2, $P = 0.09$). However, the number of total piglets born per litter
153 did not differ between the OLD and YOUNG group (12.9 $\pm$ 1.1 and 12.9 $\pm$ 1.2, respectively)

154 3.2. Plasma oxytocin concentrations of oestrous sows with boar presence

155 Boar presence for 10 min brought about an increase in plasma OT concentrations of oestrous sows
156 compared with absence ($P < 0.05$, Fig 1, Table 1). During boar presence, OT concentrations in the
157 LONG group were higher than those in the SHORT group (LS means $\pm$ SE; 27.8 ± 5.5 vs. 21.4 ± 5.4 , P
158 < 0.01 , Table 1). OT concentrations were not correlated with FD, but were positively correlated with
159 parity over the total period ($r_s = 0.31$, $P < 0.0001$). Parity class (YOUNG vs. OLD) per se did not affect
160 the OT levels during all sampling periods (Table 1), but sows in the YOUNG group with short FD
161 tended to have the lowest OT levels post boar presence ($P = 0.07$, Fig 1, Table 1). Among YOUNG
162 group, the OT levels were higher in LONG than in SHORT during and post boar presence ($P < 0.001$
163 and $P < 0.01$, respectively), whereas in the OLD group, those were not affected by FD in all sampling
164 periods (Table 1).

165 3.3. Follicle development of oestrous sows

166 FD and parity of the sow did not affect days of weaning-to-oestrus interval and when the five largest
167 preovulatory follicles reached their maximum size between three days after weaning and ovulation
168 (Table 2).

169 Mean diameters of the five largest follicles of the LONG sows tended to be larger than those of
170 SHORT sows four days after weaning ($P = 0.06$), but did not differ on other days (Table 2). Diameters
171 of the follicles of sows in the OLD group tended to be larger five days after weaning, or were larger
172 when follicles reached their maximum size after weaning until ovulation compared with those of sows
173 in the YOUNG group ($P = 0.07$, $P = 0.02$, respectively, Table 2).

174 The mean diameters of the five largest follicles measured at five days after weaning and when the
175 follicles reached their maximum size after weaning were weakly correlated with OT concentrations of
176 the oestrous sows during the total period ($r_s = 0.23$, $P < 0.0001$ and $r_s = 0.38$, $P < 0.0001$, respectively,

177 Fig 2), and these were also even more moderately correlated with parity of the sow ($r = 0.61$, $P < 0.01$
178 and $r = 0.57$, $P < 0.01$, respectively, Fig 3).

179

180 4. Discussion

181 Average FD in the current study was relatively short compared with that reported by Björkman et al.
182 (2017) from our research station (358 vs. 411 min). This might be related to the relatively low average
183 number of total piglets born in the present experiment (13.4 vs. 16.3 piglets/litter), since large litter size
184 was associated with prolonged farrowing (Fraser et al., 1997; Herpin et al., 1996; Van Rens and Van
185 der Lende, 2004).

186 Several studies showed that parity did not affect FD (Fahmy and Friend, 1981; Oliviero et al., 2010;
187 Van Dijk et al., 2005). In contrast, the results of the present study are in accordance with others
188 demonstrating that FD increases as sows get older (Björkman et al., 2017; Borges et al., 2005; Cronin
189 et al., 1993; Pejsak, 1984). This association between higher parity and longer FD has been suggested to
190 be due to large litter size (Borges et al., 2005; Dial et al., 1992), higher body condition score (Oliviero
191 et al., 2008), or/and degradation of myometrial activity (Pejsak, 1984). In the current study, however,
192 we did not establish a relationship between parity per se and litter size. In addition, body frames and
193 myometrial activity of sows were not measured in the present study. Therefore, no conclusion on the
194 cause of the association between higher parity and longer FD in the current study can be drawn.

195 Previous studies established relationships between prolonged farrowing and decreased OT release
196 during parturition in sows (Castrén et al., 1993b; Jarvis et al., 2004; Lawrence et al., 1997; Oliviero et
197 al., 2008). It was determined that considerable pain and distress during the parturition period was even
198 increased by prolonged farrowing (Mainau and Manteca, 2011; Rutherford et al., 2013), which in turn

199 inhibited OT secretion in sows (Carter, 1992; Lawrence et al., 1997; Rutherford et al., 2013). We
200 therefore considered that this association would result in reduced plasma OT concentrations of the sows
201 during subsequent insemination. In contrast to one hypothesis, however, we found that prolonged
202 farrowing was associated with higher OT concentrations of the subsequent oestrous sows in the
203 YOUNG group when standing reflex was triggered by boar introduction.

204 Irrespective of FD, the current findings corroborate those of Langendijk et al. (2003), demonstrating
205 that OT concentrations of oestrous sows peak in response to boar introduction. In the current study, the
206 back and flank of the sows were stimulated by samplers while the sows had nose-to-nose contact with a
207 boar. Langendijk et al. (2005), however, suggested that stimulation of the back and flank of sows
208 without boar introduction may not affect the release of OT, while Mattioli et al. (1986) reported that
209 olfactory stimulation could lead to an increase in OT concentrations of sows at insemination.
210 Therefore, it can be speculated that our findings indicate that boar odour, potentially accompanied by
211 presence of a boar, may make a greater contribution to elevating OT concentrations than sole
212 stimulation of the back and flank of oestrous sows during the insemination period.

213 Follicular development in the present study could represent another explanation for the relationship
214 between prolonged farrowing and increased OT concentrations and their interactions with parity in
215 oestrous sows. The present results indicate that tendencies for larger follicles, seen in the LONG group
216 and in the OLD group on day four or five after weaning respectively, could have originated from higher
217 OT concentrations of the oestrous sows. It is suggested that the production and the release of OT is
218 stimulated by oestrogen (Gimpl and Fahrenholz, 2001; Wathes et al., 1996) which can be produced
219 from follicles (Carter, 1992). Furthermore, levels of oestrogen were positively correlated with density
220 of OT receptors in the myometrium (Hoang-Vu, 1987; Okano and Okuda, 1996). It can therefore be

221 speculated that the larger follicles in older sows and in sows with prolonged farrowing may produce
222 more estradiol, which in turn could influence an increase in OT concentration.

223 The size of the largest follicles of the oestrous sows measured in the present study was estimated to be
224 similar to the size of ovulated follicles. The current results may support the previous findings of
225 Langendijk et al. (2000) and Gerritsen et al. (2008) confirming that primiparous sows had smaller
226 follicles than multiparous sows at weaning (on average 2.5 vs. 3.3 mm), and ovulation (on average 7
227 vs. 8 mm). The effects of parity on follicular development and endocrine profiles after weaning could
228 be due to the negative energy balance caused by lactation weight loss (Soede et al., 2011; Soede and
229 Kemp, 2015). Younger sows appeared more sensitive to lactation weight loss than older sows (Hoving
230 et al., 2011; Thaker and Bilkei, 2005). Clowes et al. (2003) also demonstrated the negative effects of
231 body protein loss during lactation on follicular size, follicular fluid and estradiol-17 β after weaning.
232 Therefore, the smaller size of the maximal follicles seen in the YOUNG sows in the present study is
233 presumably linked to sow metabolism during lactation. However, further studies are needed to
234 investigate the causal relationship between metabolic status during lactation and follicular development
235 after weaning.

236

237 5. Conclusions

238 Contrary to an expectation of the present study, there was a positive association between farrowing
239 duration and oxytocin concentrations at subsequent oestrus among YOUNG sows. On the other hand,
240 we found that both farrowing duration and the oxytocin levels at oestrus increased as sows got older. In
241 addition, our results suggest that the positive associations between the oxytocin levels and diameters of
242 the follicles at oestrus were also originated from parity. Therefore, we conclude that plasma oxytocin

243 concentrations and follicular development of oestrous sows are associated due to parity but difficult to
244 be predicted from the duration of previous farrowing.

245

246 Acknowledgements

247 This study was funded by the Finnish Ministry of Agriculture (MMM, grant no: 2017/312/2011),
248 Mercedes-Zacharias Research Foundation, Hankkija, Vetcare, Figen, Atria and Finnish Foundation of
249 Veterinary Research. The authors thank Merja Pöytäkangas (lab technician) for help with the oxytocin
250 analyses.

251

252 Conflict of interest statement

253 None.

254

255 References

256 Björkman, S., Oliviero, C., Rajala-Schultz, P., Soede, N., and Peltoniemi, O. (2017). The effect of litter
257 size, parity and farrowing duration on placenta expulsion and retention in sows. *Theriogenology* 92, 36-
258 44.

259 Borges, V., Bernardi, M., Bortolozzo, F., and Wentz, I. (2005). Risk factors for stillbirth and foetal
260 mummification in four Brazilian swine herds. *Preventive Veterinary Medicine*. 70, 165-176.

261 Breuel, K., Lewis, P., Schrick, F., Lishman, A., Inskeep, E., and Butcher, R.. (1993). Factors affecting
 262 fertility in the postpartum cow: role of the oocyte and follicle in conception rate. *Biology of*
 263 *Reproduction*, 48, 655-661.

264 Carter, C. (1992). Oxytocin and sexual behavior. *Neuroscience and Biobehavioral Reviews*, 16, 131-
 265 144.

266 Castrén, H., Algers, B., De Passillé, A., Rushen, J., and Uvnäs-Moberg, K. (1993a). Early milk
 267 ejection, prolonged parturition and periparturient oxytocin release in the pig. *Animal Science*, 57, 465-
 268 471.

269 Castrén, H., Algers, B., De Passille, A., Rushen, J., and Uvnäs-Moberg, K. (1993b). Preparturient
 270 variation in progesterone, prolactin, oxytocin and somatostatin in relation to nest building in sows.
 271 *Applied Animal Behaviour Science*, 38, 91-102.

272 Clowes, E., Aherne, F., Foxcroft, G., and Baracos, V. (2003). Selective protein loss in lactating sows is
 273 associated with reduced litter growth and ovarian function. *Journal of Animal Science*, 81, 753-764.

274 Cronin, G., Schirmer, B., McCallum, T., Smith, J., and Butler, K. (1993). The effects of providing
 275 sawdust to pre-parturient sows in farrowing crates on sow behaviour, the duration of parturition and the
 276 occurrence of intra-partum stillborn piglets. *Applied Animal Behaviour Science*, 36, 301-315.

277 Dial, G., Marsh, W., Polson, D., and Vaillancourt, J. (1992). Reproductive failure: differential
 278 diagnosis. *Diseases of swine* 7, 88-137.

279 Fahmy, M., and Friend, D. (1981). Factors influencing, and repeatability of the duration of farrowing in
 280 Yorkshire sows. *Canadian Journal of Animal Science*, 61, 17-22.

281 Fraser, D., Phillips, P. and Thompson, B. (1997). Farrowing behaviour and stillbirth in two
 282 environments: an evaluation of the restraint-stillbirth hypothesis. *Applied Animal Behaviour Science*,
 283 55, 51-66.

284 Gerritsen, R., Soede, N., Langendijk, P., Dieleman, S., Hazeleger, W., and Kemp, B. (2008). Peri-
 285 oestrus Hormone Profiles and Follicle Growth in Lactating Sows with Oestrus Induced by Intermittent
 286 Suckling. *Reproduction in Domestic Animals*, 43, 1-8.

287 Gilbert, C., Burne, T., Goode, J., Murfitt, P., and Walton, S. (2002). Indomethacin blocks pre-partum
 288 nest building behaviour in the pig (*Sus scrofa*): effects on plasma prostaglandin F metabolite, oxytocin,
 289 cortisol and progesterone. *Journal of Endocrinology*, 172, 507-517.

290 Gimpl, G., and Fahrenholz, F. (2001). The oxytocin receptor system: structure, function, and
 291 regulation. *Physiological reviews*, 81, 629-683.

292 Gu, Z., Gao, Y., Lin, B., Zhong, Z., Liu, Z., Wang, C., and Li, B. (2011). Impacts of a freedom
 293 farrowing pen design on sow behaviours and performance. *Preventive Veterinary Medicine*, 102, 296-
 294 303.

295 Herpin, P., Le Dividich, J., Hulin, J., Fillaut, M., De Marco, F., and Bertin, R. (1996). Effects of the
 296 level of asphyxia during delivery on viability at birth and early postnatal vitality of newborn pigs.
 297 *Journal of Animal Science*, 74, 2067-2075.

298 Higuchi, T., Honda, K., Fukuoka, T., Negoro, H., and Wakabayashi, K. (1985). Release of oxytocin
 299 during suckling and parturition in the rat. *Journal of Endocrinology*, 105, 339-346.

300 Hoang-Vu, C. (1987). Elektrische Aktivität des Myometriums beim Schwein während des Zyklus und
 301 ihre Beeinflussung durch Infusion von Östrogenen in das Uteruslumen am Tag der Rausche. *Thesis*,
 302 Hohenheim University (Germany).

303 Hoving, L., Soede, N., Graat, E., Feitsma, H., and Kemp, B. (2011). Reproductive performance of
 304 second parity sows: Relations with subsequent reproduction. *Livestock Science*. 140, 124-130.

305 Jarvis, S., Reed, B., Lawrence, A., Calvert, S., and Stevenson, J. (2004). Peri-natal environmental
 306 effects on maternal behaviour, pituitary and adrenal activation, and the progress of parturition in the
 307 primiparous sow. *Animal Welfare*, 13, 171-181.

308 Kemp, B., Soede, N., and Langendijk, P. (2005). Effects of boar contact and housing conditions on
 309 estrus expression in sows. *Theriogenology*, 63, 643-656.

310 Langendijk, P., Van den Brand, H., Soede, N., and Kemp, B. (2000). Effect of boar contact on
 311 follicular development and on estrus expression after weaning in primiparous sows. *Theriogenology*,
 312 54, 1295-1303.

313 Langendijk, P., Bouwman, E., Schams, D., Soede, N., and Kemp, B. (2003). Effects of different sexual
 314 stimuli on oxytocin release, uterine activity and receptive behavior in estrous sows. *Theriogenology*,
 315 59, 849-861.

316 Langendijk, P., Soede, N., and Kemp, B. (2005). Uterine activity, sperm transport, and the role of boar
 317 stimuli around insemination in sows. *Theriogenology*, 63, 500-513.

318 Lawrence, A., McLean, K., Jarvis, S., Gilbert, C., and Petherick, J. (1997). Stress and parturition in the
 319 pig. *Reproduction in Domestic Animals*, 32, 231-236.

320 Mainau, E., and Manteca, X. (2011). Pain and discomfort caused by parturition in cows and sows.
 321 *Applied Animal Behaviour Science*, 135, 241-251.

322 Mattioli, M., Galeati, G., Conte, F., and Seren, E. (1986). Effect of 5 α -androst-16-en-3-one on oxytocin
 323 release in oestrous sows. *Theriogenology* 25, 399-403.

324 Nayudu, P., and Osborn, S. (1992). Factors influencing the rate of preantral and antral growth of mouse
 325 ovarian follicles in vitro. *Journal of Reproduction and Fertility*, 95, 349-362.

326 Okano, A. and Okuda, K. (1996). Oxytocin receptors in the porcine myometrium during the estrous
 327 cycle and early pregnancy. *Nihon Chikusan Gakkaiho* 67, 102-103.

328 Oliviero, C., Heinonen, M., Valros, A., Hälli, O., and Peltoniemi, O. (2008). Effect of the environment
 329 on the physiology of the sow during late pregnancy, farrowing and early lactation. *Animal*
 330 *Reproduction Science*, 105, 365-377.

331 Oliviero, C., Heinonen, M., Valros, A., and Peltoniemi, O. (2010). Environmental and sow-related
 332 factors affecting the duration of farrowing. *Animal Reproduction Science*, 119, 85-91.

333 Oliviero, C., Kothe, S., Heinonen, M., Valros, A., and Peltoniemi, O. (2013). Prolonged duration of
 334 farrowing is associated with subsequent decreased fertility in sows. *Theriogenology*, 79, 1095-1099.

335 Pedersen, L., Jørgensen, E., Heiskanen, T., and Damm, B. (2006). Early piglet mortality in loose-
 336 housed sows related to sow and piglet behaviour and to the progress of parturition. *Applied Animal*
 337 *Behaviour Science*, 96, 215-232.

338 Pejsak, Z. (1984). Some pharmacological methods to reduce intrapartum death of piglets. *Pig News and*
 339 *Information*.

340 Rutherford, K., Baxter, E., D'Eath, R., Turner, S., Arnott, G., Roehe, R., Ask, B., Sandoe, P. Moustsen,
 341 V., Thorup, F., and Edwards, S. (2013). The welfare implications of large litter size in the domestic pig
 342 I: biological factors. *Animal Welfare*, 22, 199-218.

343 Sheldon, I., and Dobson, H. (2004). Postpartum uterine health in cattle. *Animal Reproduction Science*,
 344 82, 295-306.

345 Soede, N., Langendijk, P., and Kemp, B. (2011). Reproductive cycles in pigs. *Animal Reproduction*
 346 *Science*, 124, 251-258.

347 Soede, N., and Kemp, B. (2015). Best practices in the lactating and weaned sow to optimize
 348 reproductive physiology and performance. In *The gestating and lactating sow*. pp. 99-106. (Press:
 349 Wageningen Academic Publishers).

350 Taverne, M., Naaktgeboren, C., Elsaesser, F., Forsling, M., Van der Weyden, G., Ellendorff, F., and
 351 Smidt, D. (1979). Myometrial electrical activity and plasma concentrations of progesterone, estrogens
 352 and oxytocin during late pregnancy and parturition in the miniature pig. *Biology of Reproduction*, 21,
 353 1125-1134.

354 Thaker, M., and Bilkei, G. (2005). Lactation weight loss influences subsequent reproductive
 355 performance of sows. *Animal Reproduction Science*, 88, 309-318.

356 Van den Brand, H., Dieleman, S., Soede, N., and Kemp, B. (2000). Dietary energy source at two
 357 feeding levels during lactation of primiparous sows: I. Effects on glucose, insulin, and luteinizing
 358 hormone and on follicle development, weaning-to-estrus interval, and ovulation rate. *Journal of Animal*
 359 *Science*, 78, 396-404.

360 Van Dijk, A., Van Rens, B., Van der Lende, T., and Taverne, M. (2005). Factors affecting duration of
 361 the expulsive stage of parturition and piglet birth intervals in sows with uncomplicated, spontaneous
 362 farrowings. *Theriogenology*, 64, 1573-1590.

363 Van Leeuwen, J., Williams, S., Martens, M., Jourquin, J., Driancourt, M., Kemp, B., and Soede, N.
 364 (2011). The effect of different postweaning altrenogest treatments of primiparous sows on follicular
 365 development, pregnancy rates, and litter sizes. *Journal of Animal Science*, 89, 397-403.

366 Van Rens, B., and Van der Lende, T. (2004). Parturition in gilts: duration of farrowing, birth intervals
367 and placenta expulsion in relation to maternal, piglet and placental traits. *Theriogenology*, 62, 331-352.

368 Wathes, D., Mann, G., Payne, J., Riley, P., Stevenson, K., and Lamming, G. (1996). Regulation of
369 oxytocin, oestradiol and progesterone receptor concentrations in different uterine regions by oestradiol,
370 progesterone and oxytocin in ovariectomized ewes. *Journal of Endocrinology*, 151, 375-393.

371 Yun, J., Swan, K., Oliviero, C., Peltoniemi, O., and Valros, A. (2015). Effects of prepartum housing
372 environment on abnormal behaviour, the farrowing process, and interactions with circulating oxytocin
373 in sows. *Applied Animal Behaviour Science*, 162, 20-25.

374 Yun, J., Björkman, S., Pöytäkangas, M., and Peltoniemi, O. (2017). The effects of ovarian biopsy and
375 blood sampling methods on salivary cortisol and behaviour in sows. *Research in Veterinary Science*,
376 114, 80-85.

377

Table 1. The effects of farrowing duration and parity on the plasma oxytocin concentrations of sows during post-weaning oestrus in presence of a boar[†].

Period [‡]	YOUNG		OLD		<i>P value</i>		
	SHORT	LONG	SHORT	LONG	<i>FD</i> [§]	<i>Parity</i> [¶]	<i>FD*parity</i>
	(n = 9)	(n = 5)	(n = 5)	(n = 11)			
-15 to -5 min	13.8 ± 1.5	14.8 ± 1.7	13.7 ± 1.7	13.3 ± 1.6	0.79	0.76	0.48
0 to 10 min	18.6 ± 7.6	28.9 ± 7.8	24.2 ± 7.8	27.6 ± 7.7	< 0.01	0.84	0.13
15 to 60 min	13.7 ± 2.5	16.8 ± 2.6	16.6 ± 2.7	16.2 ± 2.6	0.58	0.79	0.07
-15 to 60 min	16.9 ± 2.5 ^b	19.7 ± 2.6 ^a	18.8 ± 2.6 ^{ab}	18.8 ± 2.5 ^{ab}	0.44	0.91	0.04

[†] Values represent LS means ± SEM of plasma oxytocin concentrations of the sows (total n = 30).

[‡] Repeated measures carried out on the values over four periods: 1) -15, -10 and -5 min before boar presence, 2) 0, 1, 2, 3, 4, 6, 8 and 10 min during 10 min of boar presence, 3) 15, 20, 25, 30, 40, 50 and 60 min after boar presence, and 4) total period.

[§]FD (farrowing duration) was divided into two classes: 1) SHORT: between 103 and 192 min, and 2) LONG: between 326 and 878 min.

[¶]Parity was divided into two classes: 1) YOUNG: between 1 and 3, and 2) OLD: between 4 and 11.

^{a,b}Different letters indicate that variables were significantly different at $P < 0.05$.

389 Table 2. The effects of farrowing duration and parity on follicular development and weaning to oestrus
390 intervals of subsequent oestrous sows.

	YOUNG		OLD		<i>P value</i>		
	SHORT	LONG	SHORT	LONG	<i>FD</i> [†]	<i>Parity</i> [‡]	<i>FD*parity</i>
	(n = 9)	(n = 5)	(n = 5)	(n = 11)			
Days [§]							
WOI	5.0 ± 0.2	5.4 ± 0.2	5.1 ± 0.2	4.8 ± 0.2	0.79	0.32	0.10
Maximum	4.0 ± 0.4	4.4 ± 0.5	4.7 ± 0.5	4.7 ± 0.4	0.77	0.38	0.61
Diameters, mm [¶]							
Day 3	4.5 ± 0.4	5.0 ± 0.6	4.8 ± 0.5	5.5 ± 1.0	0.56	0.42	0.81
Day 4	5.5 ± 0.3	5.9 ± 0.5	5.1 ± 0.5	5.9 ± 0.6	0.06	0.83	0.65
Day 5	5.5 ± 0.3	5.8 ± 0.3	6.1 ± 0.3	6.2 ± 0.2	0.44	0.07	0.65
Oestrus	6.0 ± 0.4	5.3 ± 0.4	5.7 ± 0.4	6.3 ± 0.3	0.84	0.30	0.10
Maximum	5.7 ± 0.2	5.6 ± 0.3	6.2 ± 0.3	6.2 ± 0.2	0.80	0.02	0.95

391 [†]FD (farrowing duration) was divided into two groups: 1) SHORT: between 103 and 192 min, and 2)
392 LONG: between 326 and 878 min.

393 [‡]Parity was divided into two groups: 1) YOUNG: between 1 and 3, and 2) OLD: between 4 and 11.

394 [§]Values represent LS means ± SE of the days for 1) weaning-to-oestrus interval, and 2) when the 5
395 largest follicles reached their maximum size after weaning until ovulation.

396 [¶]Values represent LS means ± SE of the mean diameters of the five largest follicles measured 1) on day
397 3, 2) on day 4 and 3) on day 5 after weaning until ovulation, 4) at oestrus in which the sow showed a

398 standing response to the back test, and 5) when the follicles reached their maximum size after weaning
399 until ovulation.

400

401

402 Figure 1. Plasma OT concentrations (LS means and SE) of oestrous sows in boar presence are plotted
 403 by SHORT-YOUNG (n = 9), SHORT-OLD (n = 5), LONG-YOUNG (n = 5) and LONG-OLD (n = 11)
 404 groups, according to farrowing duration and parity classes. The red shading indicates 10 min of boar
 405 presence.

406

407

408 Figure 2. Average plasma oxytocin concentrations of the sows during the total sampling period, i.e. -
 409 15 to +60 min from beginning of 10 min of boar presence, and follicle diameters measured at five days
 410 after weaning and when the follicles reached their maximum size after weaning until ovulation are
 411 indicated with Spearman correlation coefficients (r_s) ($n = 30$). Correlations were determined by
 412 repeated measures.

413

414

415 Figure 3. Parity of the sows and follicle diameters measured at five days after weaning and when the
 416 follicles reached their maximum size after weaning until ovulation are indicated with Pearson
 417 correlation coefficients (r) ($n = 30$).

418