

JUSTIFICATION OF UNILATERAL HYSTERECTOMY-OVARIECTOMY AS A MODEL TO EVALUATE UTERINE CAPACITY IN SWINE^{1,2}

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ABSTRACT

Experimental objectives were to measure the effect of ovulation rate on litter size at 86 d of gestation and at farrowing in 110 unilaterally hysterectomized-ovariectomized (UHO) gilts and in 142 intact, control gilts and to evaluate postnatal survival and development of progeny. Surgery (UHO) was performed on gilts 8 to 12 d following first estrus. Control and UHO gilts were mated and then randomly assigned to be slaughtered at d 86 of gestation or allowed to farrow. Gilts scheduled to farrow were observed by laparoscopy on d 40 of gestation to count corpora lutea (CL). Ovulation rate (number of CL) was similar for control (12.1 CL) and UHO (11.9 CL) gilts, thus indicating that compensatory ovarian hypertrophy had occurred in UHO gilts and resulted in a near doubling of ova per uterine horn relative to control gilts. Average litter size at 86 d of gestation and farrowing was greater ($P < .01$) for control than UHO gilts. At farrowing, litter size for control and UHO gilts was $9.0 \pm .3$ and $5.7 \pm .3$ pigs, respectively. Fetal losses were greater and pig weights at birth were less in litters by UHO gilts. Postnatal pig survival, growth rate to 14 d of age and 14-d individual pig weight did not differ for progeny of control and UHO gilts, and performance of UHO progeny did not appear to compromise the usefulness of this animal model. Regression of litter size on ovulation rate was $.41 \pm .15$ pigs/CL for UHO and $.60 \pm .12$ pigs/CL for control gilts at d 86 of gestation. Regression was $.07 \pm .17$ pigs/CL for UHO and $.42 \pm .14$ pigs/CL for control gilts at farrowing. Averaged over time of evaluation, regression of litter size on ovulation rate was smaller ($P < .05$) in UHO gilts ($.24 \pm .12$ pigs/CL) than in control gilts ($.51 \pm .10$ pigs/CL). Litter size of UHO gilts at farrowing approached independence from ovulation rate, therefore the UHO procedure may allow estimation of uterine capacity per uterine horn unfounded by ovulation rate.

(Key Words: Pigs, Ovulation, Uterus, Fetal Death, Litter Size.)

Introduction

Improvement of litter size in swine is hindered by the number of component traits and the sequential nature of their occurrence (i.e., ovulation, fertilization, embryonic mortality and uterine capacity). Ovulation rate has been increased through superovulation regimens (see

review by Anderson and Melampy, 1972) and by direct selection for ovulation rate (Zimmerman and Cunningham, 1975). Achievement of greater ovulation rate has increased the number of embryos at d 30 of gestation. However, litter size at parturition has not been increased significantly. These findings suggest that uterine capacity must also be improved to increase litter size. Uterine capacity includes such factors as space, nutrients, gaseous exchange and placental surface (Webel and Dziuk, 1974). In this paper, uterine capacity is defined as the maximum number of fetuses that the dam is able to support at a specific stage of gestation.

Prior to d 30 of gestation, the effects of uterine capacity are likely insignificant within the normal range of ovulation rate, but may become increasingly important as gestation progresses (Dziuk, 1968). Measurement of uterine capacity therefore requires that dams be

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challenged by more embryos at d 30 of gestation than can be nurtured to parturition. The procedures of superovulation (Day et al., 1967; Dziuk, 1968; Longenecker and Day, 1968; Christenson et al., 1973; Webel and Dziuk, 1974), embryo transfer (Dziuk, 1968; Pope et al., 1972), embryo superinduction (Dziuk, 1968) and unilateral hysterectomy-ovariectomy (UHO: Dziuk, 1968; Fenton et al., 1970; Webel and Dziuk, 1974; Knight et al., 1977) may be used to increase the number of embryos per uterine horn at d 30 of gestation. Due to failure of some gilts to respond to exogenous hormone treatment and to greater labor and donor gilt requirements for embryo transfer, the UHO procedure was chosen to study uterine capacity in the present experiment.

Previous UHO studies (Dziuk, 1968; Fenton et al., 1970; Webel and Dziuk, 1974) emphasized the effect of uterine space on litter size early in gestation. The relationship between litter size and ovulation rate was not quantified in these studies. Present experimental objectives are: 1) to determine if litter size is less dependent on ovulation rate at 86 d of gestation and at parturition in UHO gilts than in control gilts, 2) to evaluate postnatal survival and development of piglets born to UHO gilts, thereby assessing the practicality of using the UHO model to select for uterine capacity and 3) to test if litter size of UHO gilts estimates the litter size per uterine horn of intact gilts with high ovulation rates.

Materials and Methods

Two hundred and eighty-six crossbred gilts (Yorkshire × Landrace × Chester White × Large White) were checked daily for estrus beginning at 25 wk of age. As gilts expressed estrus, they were assigned randomly to control and UHO treatments at a 6:5 ratio, respectively. On d 8 to 12 following first estrus, the 110 UHO gilts were anesthetized with sodium thiopental (1 g); anesthesia was maintained with a closed circuit system of halothane and oxygen. Through a midventral incision, the left or right ovary and adjacent uterine horn were removed on an alternating basis. During a 62-d breeding season, 129 control and 104 UHO gilts were mated on the first and second day of estrus. Bred gilts within each group were randomly assigned to be slaughtered at 86 (81 to 93) d of gestation or to be farrowed. This factor is hereafter referred to as time-of-evaluation.

At 40 d of gestation, control and UHO gilts scheduled to farrow were observed by laparoscopy according to the method of Wildt et al. (1973). This procedure was modified for determining ovulation rate in gestating gilts. In addition to a 180° laparoscope (10 mm diameter) and a 5-mm, 46-cm-long tactile probe, a third trocar-cannula was passed through the abdominal wall for insertion of a 5-mm, 45-cm-long forceps for grasping the oviduct in order to position the ovary above the gravid uterus, which permitted counting the number of corpora lutea (CL).

At slaughter, ovulation rate (number of CL), number and weight of fetuses and number of mummified fetuses were recorded. At farrowing, number and weight of fully-formed pigs and number of mummified fetuses were recorded. Progeny of gilts that farrowed were weighed at 14 d of age and postnatal survival and average daily gain to 14 d of age were calculated.

Statistical Procedures. Data were analyzed using least-squares procedures as described by Harvey (1979). Ovulation rate, number of mummified fetuses, litter size, litter size at 14 d of age and postnatal survival traits were analyzed using fixed model analysis of variance procedures. The statistical model for ovulation rate, number of mummified fetuses and litter size included the effects of treatment, time-of-evaluation and their interaction. The statistical model for postnatal survival and litter size at 14 d of age included only the effect of treatment. Traits measured on individual pigs (fetal or neonatal pig weight, average daily gain and 14-d weight) were analyzed using mixed model analysis of variance procedures. The statistical model for fetal or neonatal pig weight included the fixed effects of treatment, time-of-evaluation, sex, and treatment × time-of-evaluation, and random effect of gilt within treatment × time-of-evaluation. Fixed effects were tested against whole-plot error. The statistical model for average daily gain and 14-d weight included fixed effects of treatment, sex and treatment × sex and the random effect of gilt within treatment. Significance of treatment effects was tested by the gilt within treatment mean square.

The effect of ovulation rate on litter size was estimated by use of regression procedures. Preliminary analyses indicated a linear relationship between litter size and ovulation rate; therefore, linear regressions were fitted separately for each subclass. The total data set was fitted

to a model that tested homogeneity among the four subclass regressions. The treatment \times time-of-evaluation interaction did not significantly affect regression of litter size on ovulation rate. Consequently, the difference between treatment regressions, averaged over time-of-evaluation, was evaluated with a one-tailed test because UHO treatment was expected to decrease regression of litter size on ovulation rate relative to regression for control treatment. Likewise, the difference between time-of-evaluation regressions, averaged over treatments, was also evaluated with a one-tailed test. Regression for gilts at farrowing was expected to be less than regression for gilts at slaughter due to fetal loss during late gestation.

Results and Discussion

Least-squares means for ovulation rate, number of mummified fetuses, litter size and fetal or neonatal pig weight are summarized in table 1. Ovulation rate was similar for control and UHO gilts, indicating that compensatory ovarian hypertrophy had occurred in the UHO gilts, as reported by Brinkley et al. (1964) and Dziuk (1968). Ovulatory compensation for the UHO gilts was 98% of the control gilts. Thus,

the UHO model nearly doubled the number of ova per uterine horn relative to control gilts. Counting of CL by the laparoscope method resulted in a mean similar to that of counting CL from dissected ovaries of slaughtered gilts.

Overall, the least-squares mean of litter size at 86 d of gestation and farrowing was greater ($P < .01$) for control than for UHO gilts ($9.3 \pm .2$ vs $6.3 \pm .2$ pigs, respectively). But litter size of UHO gilts was 68% of the mean litter size of control gilts, rather than 50%. At farrowing, litter size for control and UHO gilts was $9.0 \pm .3$ and $5.7 \pm .3$ pigs, respectively. Litter size of UHO gilts was 63% of the mean litter size of control gilts, which is similar to the value of 57% reported by Fenton et al. (1970) for UHO and intact gilts sacrificed at 105 d of gestation. The results indicate that at current ovulation rates in these populations of gilts, ovulation rate is one factor limiting litter size.

Average litter size decreased ($P < .01$) from $8.3 \pm .2$ pigs at 86 d of gestation (slaughter) to $7.3 \pm .2$ pigs at farrowing (table 1). This reduction in litter size is partially accounted for by the .24 mummified fetuses per gilt at farrowing. In addition, average ovulation rate as determined by laparoscope procedure was lower, .4 CL, in the animals allowed to farrow. As

TABLE 1. LEAST-SQUARES MEANS FOR OVULATION RATE, NUMBER OF MUMMIFIED FETUSES, LITTER SIZE AND PIG WEIGHT BY TREATMENT, TIME-OF-EVALUATION AND THEIR INTERACTION^a

Item	No. of gilts	Ovulation rate	No. of mummified fetuses	Litter size	Fetal and neonatal pig wt, g
Treatment (T)					
Control	115	$12.1 \pm .2$	$.22 \pm .07$	$9.3 \pm .2$	957 ± 16
UHO	84	$11.9 \pm .2$	$.50 \pm .08$	$6.3 \pm .2$	816 ± 24
Probability ^b		.40	< .01	< .01	< .01
Time-of-evaluation (TE)					
Slaughter	83	$12.2 \pm .2$	$.48 \pm .08$	$8.3 \pm .2$	498 ± 20
Farrow	116	$11.8 \pm .2$	$.24 \pm .07$	$7.3 \pm .2$	1274 ± 21
Probability ^b		.17	.02	< .01	< .01
T \times TE					
Control-slaughter	45	$12.5 \pm .3$	$.33 \pm .10$	$9.6 \pm .3$	527 ± 25
Control-farrow	70	$11.7 \pm .2$	$.11 \pm .08$	$9.0 \pm .3$	1387 ± 21
UHO-slaughter	38	$11.9 \pm .3$	$.63 \pm .11$	$6.9 \pm .4$	469 ± 32
UHO-farrow	46	$11.9 \pm .3$	$.37 \pm .10$	$5.7 \pm .3$	1162 ± 37
Probability ^b		.17	.83	.40	< .01

^aNumber of CL were recorded at slaughter (86 d of gestation) and by laparoscopy at 40 d of gestation for gilts assigned to farrowing. Number of mummified fetuses, litter size and pig weights were recorded at slaughter (86 d of gestation) and at farrowing.

^bLevel of significance of the main effect or interaction.

anticipated from data collected at 86 d of gestation and at farrowing, UHO gilts had a greater loss of fetal pigs than control gilts (1.2 vs .6 fetal pigs, respectively) during this time period. Because fetal loss occurs throughout gestation, especially in UHO gilts, uterine capacity should be measured at parturition to study the effects of uterine capacity on litter size at birth.

Additional information on number of embryos and fetuses in intact and UHO gilts at different stages of gestation was provided by Fenton et al. (1970). They reported a difference of .6 live embryos ($9.3 \pm .6$ vs $8.7 \pm .7$ embryos) at 25 d of gestation but a difference of 4.1 live fetuses ($9.6 \pm .6$ vs $5.5 \pm .5$ fetuses) at 105 d of gestation. From this comparison, it appears that litter size of UHO gilts at d 25 of gestation is similar to litter size in intact gilts. However, between d 25 of gestation and farrowing, greater fetal losses occur in UHO gilts than in intact gilts. Therefore, UHO gilts that produce larger litters at farrowing may provide a more optimum uterine environment (uterine capacity) from d 25 of gestation to farrowing than UHO gilts that produce small litters at farrowing. Greater fetal loss between d 25 or 40 of gestation and farrowing has also been reported in superovulated sows with greater numbers of embryos at d 25 and 40 of gestation (Longenecker and Day, 1968). Uterine capacity may also be evaluated successfully in intact gilts with high ovulation rates.

Interaction of treatment and time-of-evaluation was significant for fetal and neonatal pig weights (table 1). Weight of all fetal pigs increased 776 g from 86 d of gestation to farrowing, but weight of fetal pigs from control gilts increased 860 g while weight of fetal pigs from UHO gilts increased 693 g. Decreased growth rate of UHO fetuses was likely a consequence of greater fetal competition in UHO

gilts as compared with less crowded uterine conditions of control gilts, as reported by Knight et al. (1977).

Postnatal survival, growth rate to 14 d of age and 14-d individual pig weight did not differ for progeny of control and UHO gilts (table 2). Despite significantly lighter birth weights, progeny of UHO gilts tended to gain more rapidly; 14-d weights were nearly equal for progeny of gilts in both treatments. This small advantage was most likely the result of reduced competition among pigs because of the smaller litter size at birth for UHO gilts. Litters from UHO dams can be managed in the same way as litters from control dams without compromising the usefulness of this experimental animal model. The significant difference in litter size at parturition for control and UHO gilts was maintained through 14 d of age ($7.6 \pm .3$ vs $4.6 \pm .4$ pigs, respectively).

Regression of litter size on ovulation rate is illustrated in figure 1 for each treatment within time-of-evaluation subclass. Averaged over time-of-evaluation, regression of litter size on ovulation rate was smaller ($P < .05$) in UHO gilts ($.24 \pm .12$ pigs/CL) than in control gilts ($.51 \pm .10$ pigs/CL). Thus, the effect of ovulation rate on litter size was significantly reduced by use of the UHO model. In fact, regression of litter size on ovulation rate was $.07 \pm .17$ pigs/CL for UHO and $.42 \pm .14$ pigs/CL for control gilts at farrowing. Consequently, litter size of UHO gilts at farrowing approached independence of ovulation rate ($r = .06$). The UHO model seemingly allows the full expression of uterine capacity of one uterine horn. In contrast, uterine capacities of a proportion of control gilts are not realized because ovulation rates are limiting.

In control gilts, distribution of fetal survival at 86 d of gestation and at farrowing is skewed toward 100% (figure 2) and is similar to that

TABLE 2. LEAST-SQUARES MEANS FOR POSTNATAL SURVIVAL, AVERAGE DAILY GAIN, WEIGHT TO 14 D OF AGE AND 14-D LITTER SIZE

Item	Postnatal survival, %	Avg daily gain, g/d	14-d wt, kg	14-d litter size
Control	90.9 ± 2.4	164 ± 4	$3.7 \pm .1$	$7.6 \pm .3$
UHO	87.6 ± 3.0	173 ± 7	$3.6 \pm .1$	$4.6 \pm .4$
Probability ^a	.38	.23	.71	<.01

^aLevel of significance.

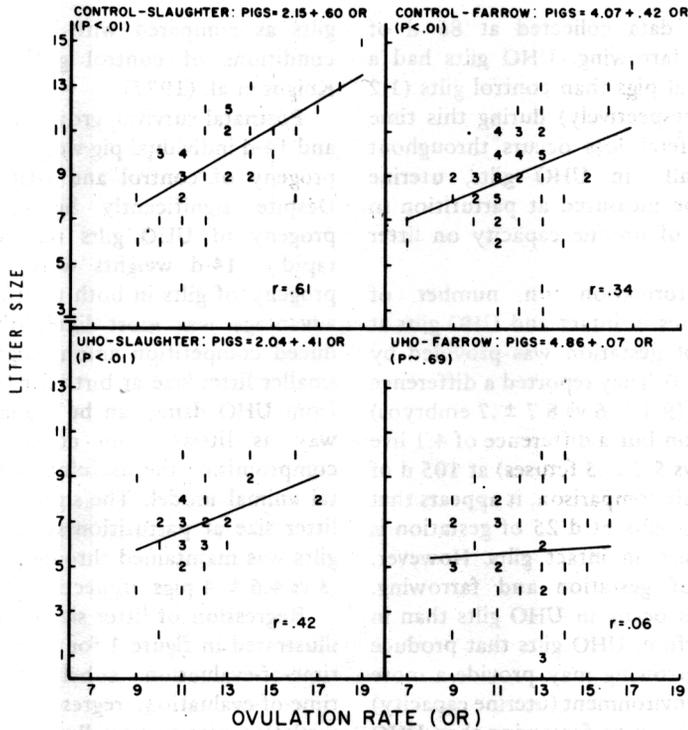


Figure 1. Relationship of ovulation rate with litter size in control and UHO gilts at slaughter (86 d of gestation) and at farrowing. Numbers in the graph represent the number of litters observed.

reported by Blichfeldt and Almlid (1982). This may occur because a certain proportion of control gilts have a greater uterine capacity than can be expressed due to limitations of ovulation

rate. These gilts, therefore, have survival rates approaching 100%. However, when ovulation rate is not limiting, as in the UHO model, distribution of fetal survival at 86 d of gestation

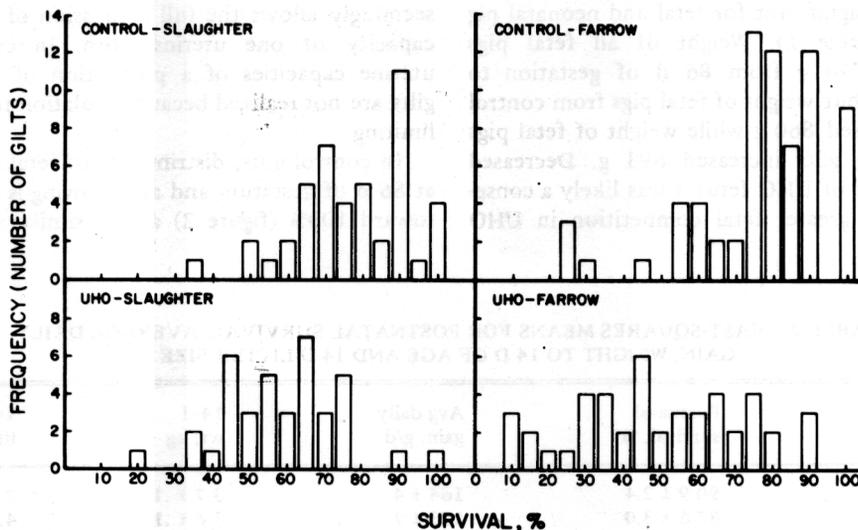


Figure 2. Frequency distribution of fetal survival in control and UHO gilts at slaughter (86 d of gestation) and at farrowing.

and at farrowing is not skewed towards 100% (figure 2) but approaches normality. This suggests that range of uterine capacity is greater than implied by variation in litter size of control gilts.

The UHO gilt provides a model that decreases the effect of ovulation rate on litter size, but it is not known if the UHO gilts simulates the litter size per uterine horn of intact gilts with high ovulation rates. To address this concern, ovulation rate and litter size data collected on UHO-farrow gilts were multiplied by 2 to scale the bivariate distribution to a total uterine basis (Leymaster et al., 1986). These scaled data were plotted with raw data collected on control-farrow gilts (figure 3). The two linear regression equations predicting litter sizes from ovulation rates are also plotted. The equation for the scaled UHO-farrow data has the same regression coefficient as presented in figure 1, but the intercept value is doubled. There is agreement between predicted litter sizes from the two equations at ovulation rates, 16 and 17, where the two data sets overlap. This agreement suggests that uterine compensation did not occur in UHO gilts and implies that UHO gilts simulate one-half the litter size of control gilts with doubled ovulation rates.

The expanded relationship of litter size with

ovulation rate (figure 3) is likely curvilinear rather than linear, as illustrated for each original data set (figure 1). Also, from a biological standpoint, litter size should approach a plateau as ovulation rate increases. Such a relationship between litter size (LS) and ovulation rate (OR) may be tested by fitting the Brody (1945) post-inflection exponential function $[LS=A(1-Be^{-K(OR)})]$ to the data. The resulting equation and graph are presented in figure 3. The estimate of A, the plateau, is 12.2 pigs and corresponds to litter size when ovulation rate is not a limiting factor. This is an estimate of the mean uterine capacity for this population of gilts. The estimate of K, a parameter without units, was .122 and K is related to the general shape of the curve. The parameter B allows the intercept to deviate from zero and was estimated to be 1.08, yielding an intercept of $-.96$ pigs.

Data reported by Johnson et al. (1984) were used to validate this nonlinear relationship between litter size and ovulation rate. Briefly, these researchers successfully selected for an increase in ovulation rate and observed a correlated response in litter size. These authors concluded that 15 to 30% of the increase in ovulation rate, from 14.5 to 19.5 CL, was represented as a fully-formed pig at birth. From

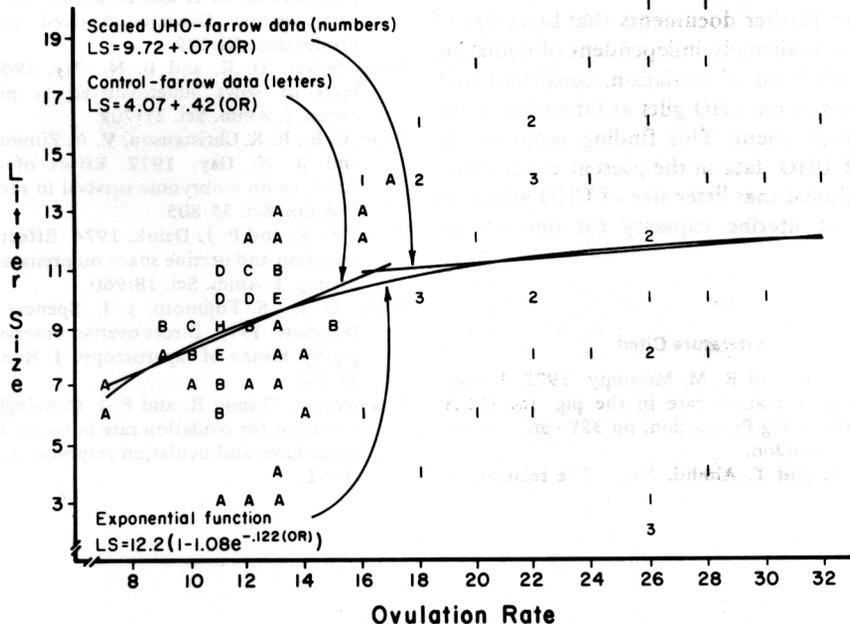


Figure 3. Relationships between litter size at birth and ovulation rate for control and scaled UHO data. Letters and numbers in the graph represent the number of litters observed (A = 1, B = 2, etc.).

the exponential function, predicted litter sizes at ovulation rates of 14.5 and 19.5 were 9.94 and 10.96 pigs, respectively. This difference of 1.02 pigs, divided by the 5-unit change in CL number, predicts that 20% of the increase in ovulation rate would be realized in increased litter size. The selection data of Johnson et al. (1984) therefore agree with the modeled, phenotypic relationship shown in figure 3.

Further validation of the UHO model for estimating uterine capacity was done by analysis of data from 259 untreated and superovulated gilts (B. N. Day, personal communication; Lamberson and Day, 1986). Natural ovulation rate of control gilts ranged from 8 to 19 CL, whereas ovulation rate of superovulated gilts ranged from 10 to 76 CL. The data were limited to ovulation rates of less than 39 CL for analysis. The relationship between litter size and ovulation rate was quantified by fitting Brody's function to the data as described previously. The resulting nonlinear function [$LS=10.8(1-1.66e^{-.185(OR)})$] explained more ($P<.01$) of the variation in litter size than did linear regression of litter size on ovulation rate. The estimate of mean uterine capacity was 10.8 pigs. Linear regression of litter size on ovulation rate ranging from 8 to 19 CL was $.38 \pm .08$ pigs/CL. From 19 to 38 CL, linear regression was $.01 \pm .09$ pigs/CL. Correlations between litter size and ovulation rate in the former and latter data sets were .33 and .02, respectively. This result further documents that litter size of intact gilts is virtually independent of ovulation rate at high levels of ovulation, consistent with data collected on UHO gilts at farrowing in the present experiment. This finding supports the scaling of UHO data in the present experiment. It is concluded that litter size of UHO gilts is an estimate of uterine capacity for one uterine horn.

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