ABSTRACT: Colostrum affects gut and uterine gland development in the neonatal piglet, suggesting that subsequent growth and reproductive performance may be affected. Measuring immunoglobulin in piglet serum using the immunoglobulin immunocrit on Day 1 of age provides a simple, inexpensive indication of the amount of colostrum acquired by the piglet in the first day of life. Relationships between serum immunoglobulin immunocrit measures and subsequent growth rates, age at puberty, incidence of puberty failure, litter size, and lactation performance were examined in pigs born and subsequently farrowing between 2009 and 2013. Immunoglobulin immunocrit measures were collected on 16,762 piglets on Day 1 of age. Of these piglets, BW measurements were available from 15,324 (7,684 males and 7,640 females) piglets at a range of ages from weaning to 200 d of age, allowing an assessment of growth rates. Age at puberty was recorded from a subset of 2,857 of the females after observing them for estrous behavior from approximately 170 to 250 d of age. To examine relationships between d 1 immunocrit and puberty failure, gilts with immunocrit measures that failed to reach puberty (n = 119) were matched with littermate gilts with immunocrit measures that achieved puberty (n = 167). Similarly, number born alive was collected on a subset (n = 799) of females from first to fourth parities for which d 1 immunocrits were measured on them as neonates. Finally, d 1 immunocrit effect on adult lactational competence was assessed by measuring litter average immunocrit (offspring of 440 females) and litter average piglet preweaning growth rate (offspring of 774 females) in females where d 1 immunocrits were available from them as neonates. Results indicated that low d 1 immunocrits were subsequently associated with reduced growth (P < 0.01), increased age at puberty (P < 0.01), reduced number born alive (P < 0.05), reduced litter average immunocrit (P < 0.05), and reduced litter average preweaning growth rate during lactation (P < 0.05). This suggests that management efforts to improve the amount of colostrum ingested by neonatal piglets would result in beneficial changes in production efficiency, particularly for gilts destined for the breeding herd. It also suggests that the immunoglobulin immunocrit can be useful in monitoring colostrum ingestion to maximize the beneficial effects of colostrum on subsequent performance.

Key words: colostrum, growth, immunocrit, lactation, litter size, puberty

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INTRODUCTION

Neonatal piglets that do not ingest colostrum have poor survival due to low energy stores (Yaguchi et al., 1980; Noblet and Le Dividich, 1981; Le Dividich et al., 1994; Vallet et al., 2013). Piglets are also born with very low levels of immunoglobulin, and colostrum immunoglobulin is transported across the gut epithelium of the piglet and into the blood (Klobasa et al., 1981, 1987; Porter and Hill, 1970). Along with neonatal nutrition and immunity, recent reports indicate that colostrum affects the development of piglet tissues, most notably the lining of the gut (Hammon et al., 2012) and the reproductive tract (Bartol et al., 2013). These effects are at least partially mediated by hormones (e.g., relaxin, IGF-1) in colostrum and are collectively termed “lactocrine” effects (Bartol et al., 2008; Baghelli et al., 2009). However, the consequences for adult performance of colostrum-induced differences in development during the neonatal period are unclear.

Because piglets are born with low levels of immunoglobulin, measurement of serum immunoglobulin provides an assessment of the amount of colostrum obtained by piglets (Yaguchi et al., 1980; Vallet et al., 2013). The immunoglobulin immunocrit, which is a simple, rapid, inexpensive method for measuring immunoglobulin in piglet serum, was developed to assess whether piglets acquired sufficient colostrum (Vallet et al., 2013). As expected, immunocrit values were correlated with stomach contents of neonatal piglets, and low immunocrit values were associated with poor survival. We have collected immunocrit measures on most piglets born in the U.S. Meat Animal Research Center (USMARC) swine herd from 2009 to 2013 to facilitate genomic analysis for this trait (Rohrer et al., 2014). The objectives of this study were to assess relationships between Day 1 piglet serum immunocrit values and subsequent growth, age at puberty, puberty failure, litter size, and lactational performance.

MATERIALS AND METHODS

Animal procedures were approved by the USMARC Institutional Animal Care and Use Committee and conform to Federation of Animal Science Societies (2010) guidelines for the care and use of agricultural animals in research.

The number born alive and individual birth and weaning weights were routinely collected for all litters born at the USMARC from November 2009 to December 2013. In addition, jugular blood samples were routinely collected from piglets that were alive on Day 1 of age and measured for the immunoglobulin immunocrit ratio as described by Vallet et al. (2013). Briefly, blood samples were allowed to clot for at least 30 min and centrifuged at 1,000 × g for 10 min at 4°C, and 50 μL serum was mixed with 50 μL 40% (wt/vol) ammonium sulfate in distilled water. The precipitated sample was loaded into a hematocrit centrifuge tube and centrifuged at full speed (12,000 × g) for 10 min at room temperature. The ratio of the length of the precipitate in the tube divided by the length of the diluted serum in the tube provides the immunocrit ratio, a quantitative measure for immunoglobulin. This resulted in 16,762 immunocrit measurements. Piglets born in 2009 and 2010 were crossbred gilts composed of Landrace, Duroc, and Yorkshire breeds. In 2011, litters were the result of mating Landrace, Duroc, York crossbred females with commercial maternal line Landrace boars. In 2012, litters were the result of mating Landrace, Duroc, York crossbred and (Landrace, Duroc, York-Landrace crossbred) females with commercial maternal line Yorkshire boars. In 2013, litters were once again the result of mating Landrace, Duroc, York crossbred, Landrace, Duroc, York-Landrace crossbred, and Landrace, Duroc, Yorkshire Landrace, York crossbred females with commercial maternal line Landrace boars. Standard management of litters at the USMARC was followed including 1) piglets were cross-fostered if litters were greater than 12 piglets born alive if suitable receiving litters were available, 2) male piglets were routinely castrated at 1 wk of age, 3) piglets received creep feed beginning on d 15 of age, and 4) piglets were weaned on approximately d 21 (2009 and 2010) or 24 (2011 to 2013).

Piglets were weighed at weaning and a subset was culled (4,477 males and 932 females). The remainder entered the nursery and remained there for approximately 4 wk, at which time they were weighed again and a subset was culled (2,150 males and 1,343 females). Gilts retained for breeding or pigs of either sex retained for finishing experiments were housed in finishing barns and fed our standard USMARC grower and finisher diets. Gilts retained for breeding were weighed again at approximately 160 to 170 d of age before being transferred to the breeding area for estrus detection. Pigs retained for finishing experiments were weighed at a variety of ages. Weights beyond the nursery stage were available for 1,057 males and 5,365 females. In all, 15,324 individual pigs (7,684 males and 7,640 females) with weight measurements and d 1 immunocrits were available for analysis.

Gilts entering the breeding area were fed 2 kg feed per day and were observed daily for estrous behavior using fence line contact with mature boars. Every incidence of standing estrous behavior was recorded and first observed incidence was used to calculate age at puberty. At approximately 250 d of age, gilts that had not been observed in standing estrus were slaughtered and
the reproductive tract visually assessed to determine whether the gilt was cycling (and so was experiencing behavioral anestrus) or not cycling (prepubertal). This resulted in 2,857 age at puberty measurements and 119 gilts that failed to reach puberty. Gilts that failed to reach puberty were matched with littermates (167) that attained puberty for subsequent analysis.

Gilts were routinely mated on their second or later estrus. Sows (first to third parity) were routinely mated on their first postweaning estrus. Females were mated by artificial insemination using up to 2 (2012 and 2013 farrowings) or 3 (2009 to 2011 farrowings) doses of semen 12 to 24 h apart, if they remained in standing estrus. This resulted in 799 individual females with both d 1 immunocrit values when they were piglets and number born alive records as adults, 440 individual females with d 1 immunocrit values as piglets and litter average immunocrit records (measured on offspring) as adults, and 774 individual females with d 1 immunocrit values and litter average preweaning growth rate records (measured on offspring) as adults, with repeated measures ranging from first to fourth parity.

Statistical Analysis

Piglet weight data were log transformed before analysis and subsequently back-transformed for presentation. Weight data were analyzed using PROC MIXED (SAS; SAS Inst. Inc., Cary, NC) with a model that included line (to adjust for breed composition), sex (barrow or gilt), the linear effect of d 1 immunocrit, the linear and quadratic effects of day of age, sex × linear effect of immunocrit interaction, sex × linear and quadratic effects of age, the interaction of the linear effect of d 1 immunocrits with the linear and quadratic effects of age, and the sex × linear effect of d 1 immunocrits × linear and quadratic effects of age. The same model was used with PROC GLM to enable the calculation of $r^2$ for the effect of the immunocrit on growth.

Age at puberty data were analyzed using PROC MIXED with a model that included the linear effect of d 1 immunocrit. To assess how well the regression line fits the immunocrit data, in a second analysis, immunocrits were grouped into categories using the following scheme: category 0.025 = immunocrits <0.05, category 0.075 = immunocrits >0.05 and <0.1, category 0.125 = immunocrits >0.1 and <0.15, category 0.175 = immunocrits >0.15 and <0.2, and category 0.225 = immunocrits >0.2. Then, PROC MIXED was used to generate least squares means for age at puberty for each immunocrit category and the means were plotted along with the regression line.

The effect of immunocrit values on puberty failure was analyzed using gilts that failed to attain puberty and their matching littermates. Analysis was done using PROC GLIMMIX modeling puberty failure as the event with a binary distribution. The model included the linear effect of d 1 immunocrit as a fixed effect and a random effect of litter.

Litter size (number born alive) data were analyzed using PROC MIXED with a model that included the linear effect of d 1 immunocrit, the fixed effect of parity, and their interaction. Dam was included as a random effect. To generate least squares means for immunocrit categories, an analysis similar to that for age at puberty was performed using PROC MIXED. The model included female, immunocrit category, and parity.

Mammary gland function was analyzed 2 ways, using litter average d 1 immunocrit data and litter average preweaning growth rate data. Preweaning growth rate was calculated for each piglet alive at weaning by subtracting birth weight from weaning weight and dividing by age at weaning. Then, a litter average was calculated for each female, after accounting for cross-fostering. Litter average immunocrit data were analyzed by PROC MIXED with a model that included the linear effect of the immunocrit, the effect of parity, and their interaction. PROC MIXED was used in a second analysis to generate least squares means for immunocrit categories as described for age at puberty and litter size. Litter average preweaning growth rate data were analyzed using PROC MIXED and a model that included the linear effect of d 1 immunocrit, parity, and their interaction. A second analysis using PROC MIXED was used to generate least squares means for immunocrit categories.

RESULTS

Growth

There was no sex × linear effect of d 1 immunocrit × linear or quadratic effect of age, so these 3-way interactions were dropped from the analysis. The linear and quadratic effects of age on BW were highly significant ($P < 0.01$) and accounted for 95% of the variation in weights. Sex ($P < 0.01$) and sex × linear and quadratic effects of age ($P < 0.01$ for both) were observed. The linear effect of d 1 immunocrit ($P < 0.01$) and the interactions of d 1 immunocrit with linear and quadratic age ($P < 0.01$ for both) were also significant. Effects of sex and the immunocrit accounted for 0.65 and 3.27%, respectively, of the variation in weights that remained after age effects were subtracted. Growth patterns for males and females with low (0 immunocrit) and high (0.20) immunocrit values are illustrated in Fig. 1. Because the analysis used the linear effect of d 1 immunocrit, the 0 and 0.20 immunocrit values were chosen to illustrate the full range of the effect of the d 1 immunocrit. The figure indicates that a low im-
Immunocrit values and performance traits

Immunocrit is associated with reduced weights throughout the growth curve for both sexes.

Age at Puberty

Age at puberty was negatively associated with d 1 immunocrit values ($P < 0.01$; Fig. 2). According to the regression line, the difference between low (0) and high (0.2) immunocrits was a reduction in age at puberty of approximately 8 d. There was no relationship between the immunocrit ratio and puberty failure ($P = 0.182$; data not shown).

Litter Size

Number born alive was affected by both parity ($P < 0.01$) and d 1 immunocrit of the dam as a neonate ($P < 0.05$) and there was no interaction. Number born alive increased from first (9.7 ± 0.1) to fourth (11.4 ± 0.2) parity. The linear effect of d 1 immunocrit of the dam as a neonate is illustrated in Fig. 3, averaged over parity. The regression indicated that the difference in number born alive for females that had a low (0) or high (0.2) immunocrit on Day 1 of age was approximately 1.4 piglets.

Lactation

Mammary gland function was examined by measuring litter average immunocrit values and litter average preweaning growth values of progeny in adulthood. There were significant effects of both parity ($P < 0.01$) and d 1 immunocrit of the dam as a neonate ($P < 0.05$) on litter average d 1 immunocrit values of the progeny. Litter average d 1 immunocrit values increased from first (0.112 ± 0.003) to fourth (0.144 ± 0.004) parity. The linear effect of d 1 immunocrit of the dam as a neonate on litter average d 1 immunocrit values of the progeny (averaged over parity) is illustrated in Fig. 4. The regression line indicated that the difference in litter average immunocrits of the progeny between females that had low (0) and high (0.2) immunocrits as neonates was 0.013. Regarding litter average preweaning growth of the progeny, after adjusting data for a highly significant negative linear effect of number weaned in the litter ($P < 0.01$), there were effects of both parity ($P < 0.01$) and d 1 immunocrit of the dam as a neonate ($P < 0.05$). Litter average preweaning growth of the progeny increased from first (0.241 ± 0.001 kg/d) to fourth (0.281 ± 0.003 kg/d) parity. The linear effect of d 1 immunocrit of the dam as a neonate on subsequent adult litter average preweaning growth rate of the progeny is illustrated in Fig. 5. The regression line indicated that the difference in litter average preweaning growth rate for dams with low (0) and high (0.2) d 1 immunocrit values as neonates was 0.016 kg/d.

**DISCUSSION**

These results indicate that the amount of colostrum obtained by piglets during the neonatal period, measured by immunocrit, influences litter size when dams reach adulthood, which is consistent with previous re-
results reported by Bartol et al. (2013) of “lactocrine” effects on neonatal uterine development. In addition to effects on uterine development, results further suggest that colostrum influences growth rate, age at puberty, and subsequent mammary gland function. Taken together, these results provide evidence that colostrum management techniques are not only valuable in terms of reducing preweaning mortality but are also likely to be important to optimize subsequent performance into adulthood. Although our results are focused primarily on reproductive performance of dams, previous results also suggest that reproductive performance of sires may also be influenced by the amount of colostrum received during the neonatal period (Rahman et al., 2014). The current results also further indicate the immunocrit is valuable for use in assessing whether piglets obtain sufficient colostrum and are likely to perform optimally, particularly for animals destined for the breeding herd.

The effects of colostrum on intestinal development during the neonatal period are well known (Wang and Xu, 1996; Thymann et al., 2006; Möller et al., 2011; Siggers et al., 2011; Hammon et al., 2012). Colostrum promotes intestinal villus height and also promotes expression of various digestive enzymes, most notably lactase (Wang and Xu, 1996; Thymann et al., 2006). Most of these experiments were done comparing colostrum to formula or other types of milk replacer and are short term, examining intestinal function within a couple weeks of birth. There appears to be no study in which the long-term effects of colostrum on intestinal function or growth have been performed, perhaps because of the difficulty and cost of measuring colostrum intake and subsequently examining pigs as they grow to adulthood. Our results indicate that d 1 colostrum intakes, measured using the immunocrit, had long-term consequences for growth rate in both males and females. Therefore, colostrum affects growth into adulthood. Moreover, the effect on growth rate was similar in scale to differences between sexes over the range of d 1 immunocrits observed. Given that colostrum affects gut development, one hypothesis is that colostrum intake is needed for full development of the digestive tract, and therefore, gut function is relatively impaired in piglets that do not obtain sufficient colostrum by d 1 of age. Alternatively, colostrum contains IGF and other hormones (Cera et al., 1987; Simmen et al., 1988) that could permanently affect the metabolism of the pig, resulting in long-term growth effects.

This is the first report of colostrum effects on age at puberty. Ingestion of colostrum, as measured using the immunocrit, reduced subsequent age at puberty by approximately 8 d over the range of immunocrit values observed. Previous reports indicate that gilts with lower growth rates reach puberty later (Kummer et al., 2009). Therefore, some of these differences could be due to the effects of colostrum on growth rate, in which gilts that grow more slowly as a result of lack of colostrum would reach puberty later. Alternatively, hormones contained within colostrum could affect brain maturation during the neonatal period that then influences puberty onset. As with growth rates, the mechanisms involved in colostrum effects on age at puberty await further investigation.

Previous reports indicate that along with gut development, ingestion of colostrum promotes early neonatal
Immunocrit values and performance traits

Figure 5. The linear effect (P < 0.05) of d 1 immunoglobulin immunocrit values of the dam as a neonate on subsequent litter average preweaning growth rate of the progeny (averaged over up to 4 parities) generated by regression analysis (line) is illustrated. The r^2 for the relationship between the immunocrit and preweaning growth rate was 0.43%. For comparison, litter size least squares means (open squares) for individual categories of d 1 immunocrit values are also illustrated along with SE (some are too small to be visible). The number of observations for each mean is in parentheses.

developmental events in uterine and testis development (Frankshun et al., 2012; Miller et al., 2013; Rahman et al., 2014). Specifically, lack of colostrum delays the onset of uterine gland development and delays hallmarks of uterine gland development such as the elaboration of estrogen receptor expression and matrix metalloproteases in neonatal uterine tissues (Chen et al., 2011; Frankshun et al., 2012; Miller et al., 2013). Administration of exogenous relaxin, which is a component of colostrum (Frankshun et al., 2009, 2011), can duplicate many of the effects of colostrum but not all of them (Bagnell et al., 2005; Yan et al., 2005, 2008; Masters et al., 2007; Bartol et al., 2009). Therefore, it appears that the effects of colostrum are mediated by relaxin and other hormones contained in colostrum. These reports have led to the development of the “lactocrine hypothesis,” where it is proposed that hormones found in colostrum affect reproductive development (Bartol et al., 2008; Bagnell et al., 2009). As with experiments examining gut development, long-term effects of colostrum on reproductive competence are limited. Our results indicate that colostrum ingestion, as measured by the immunocrit, is associated with differences in litter size of greater than a piglet per litter over the range of immunocrit values observed, and that this effect was uniform across parities up to fourth parity. Therefore, the reproductive performance of female piglets that do not receive sufficient colostrum is permanently impaired, which is consistent with the reports of impairment of uterine gland development.

It seemed likely that if neonatal uterine gland development was affected by colostrum ingestion, developmental events with regard to neonatal mammary gland development might also be affected, prompting an analysis of the effect of the immunocrit on lactational performance. We examined lactation in 2 ways. First, we used litter average immunocrits of the progeny as a measure of delivery of colostrum by the dam. Second, we used litter average piglet preweaning growth rates of the progeny as a measure of lactational performance. In both cases, lactational measures were adjusted for litter size. For both measures, increased d 1 immunocrits of dams as neonates were associated with improvements in lactational performance of the dams as adults. Litter average immunocrits were increased by approximately 10% over the range of d 1 immunocrit values observed. Similarly, litter average preweaning growth rate was increased by approximately 6% over the range of d 1 immunocrit values. The neonatal period is known to be sensitive to both hormones and biologically active agents (Fenton et al., 2012), with exposure during this time having various consequences on later mammary gland function. It seems likely that one or more hormones present in colostrum mediate improved mammary gland development shortly after birth, with consequent improvements in mammary gland function during adulthood. Alternatively, the improvements in mammary gland function observed could be a consequence of improved growth rate or earlier onset of puberty. Further investigation of neonatal mammary gland development with and without colostrum is necessary to begin to distinguish between these possibilities.

These results elevate the importance of colostrum to the physiology of the pig. Various strategies are available to manage or improve colostrum availability in routine production systems. Perhaps the most common of these are split-suckle programs, where litter sizes are manipulated to improve access to colostrum for at-risk piglets, either in terms of late-born piglets or low birth weight piglets, depending on the goals of the program (Holyoake et al., 1995). The use of the immunocrit for monitoring a split-suckle program was previously reported (Vallet, 2013), and it was found to be useful both in identifying piglets that do not receive colostrum and in demonstrating that the program was having the desired beneficial effect. Another approach to manipulating colostrum is genomic selection. Genomic markers associated with piglet immunocrits were recently reported (Rohrer et al., 2014) and these could be used to select animals for improved neonatal nursing ability. A third option might be hand feeding of colostrum; however, the logistics of collecting colostrum and providing it to piglets is likely to be economically nonviable. Nevertheless, colostrum effects on piglet survival and subsequent adult performance suggest that further research to generate strategies to
improve colostrum availability to piglets would result in improvements in production efficiencies.

In conclusion, results indicate that growth rate, age at puberty, litter size, and lactational performance are all associated with differences in d 1 immunoglobulin immunocrit ratios and, by inference, are affected by the amount of colostrum acquired by piglets at birth. Differences in adult traits between piglets receiving low versus high amounts of colostrum range from 5 to 15% depending on the trait. Although the individual benefits of colostrum on adult performance are relatively small for each trait, collectively they are likely to be important, particularly for dams destined to enter the breeding herd. An improvement in litter size of greater than 1 piglet per litter, combined with a 6% improvement in litter average preweaning growth, multiplied by the number of parities for which a sow may remain in the breeding herd for her lifetime, represents substantial benefits to production efficiency. This suggests that efforts to improve colostrum management, particularly for gilts that will enter the breeding herd, will result not only in improved preweaning survival of piglets (Vallet et al., 2013) but also in improved performance as adults. These results also support the utility of the immunoglobulin immunocrit assay for assessing whether piglets are successful in obtaining colostrum within the first day of life (Vallet, 2013; Vallet et al., 2013).

**LITERATURE CITED**


