ABSTRACT

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The objective of this study was to evaluate the genetics of functional teat number in swine. Piglet survival is of great importance for swine producers throughout the world due to its relationship with animal well-being and farm profitability. Availability and accessibility of functional teats on a sow is essential for enhancing piglet livability. Teat traits including total teat number (TT), functional teat number (FT), and non-functional teat number (NFT), were observed and recorded on 3,099 Landrace × Large White F1 sows. Variance components were estimated using AIREMLF90. Models included parity, farm, individual scorer, and phase of production as fixed effects. Means for TT, FT and NFT at farrowing were 14.93, 13.90 and 1.03, respectively, and 14.43, 13.02 and 1.15, respectively, at weaning. For farrowing, weaning and combined datasets, TT means were greater ($P<0.01$) than FT means. Heritability estimates for TT, FT and NFT ranged from 0.18 to 0.37, 0.16 to 0.28, and 0.14 to 0.18, respectively. Total teat number and functional teat number had positive genetic correlation estimates across farrowing and weaning datasets ranging from 0.68 to 0.77. Functional mammary glands had genetic correlation estimates of 0.72 and -0.57 with FT and NFT, respectively. At farrowing the genetic correlation estimate between NW and FT was positive (0.50), whereas the genetic correlation estimate between NW and NFT was negative (-0.38). An increase of one functional teat increased number of piglets weaned by 0.27. Sufficient genetic variation for total teat number and functional teat number was observed signifying that genetic improvement for these traits is possible. Results suggest that by focusing selection on functional teat number an increase in non-functional teat number can be avoided. Therefore, utilizing functional teat number in the

breeding goal should improve general teat quality and sow performance. By increasing the number of functional teats on a sow, producers can increase the number of piglets that survive to weaning and grow quickly.

The Genetics of Functional Teats in Swine

by
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BIOGRAPHY

Audrey Leah Earnhardt was born and raised in Greensboro, NC. Growing up she found passion in working with animals and playing volleyball and soccer. Her parents raised her as an avid Carolina Tar Heels fan, but after starting her undergraduate career at North Carolina State University (NCSU) to pursue her passion for animals she realized she was a wolf in sheep's clothing. During her time as an undergraduate student she worked as a research assistant on a swine nutrition trial with Dr. Mark Knauer and started working as a veterinary assistant with Banfield Pet Hospital. These experiences instilled in her an enthusiasm for research and helping animals, which has led her towards wanting to continue her research work and further her knowledge of genetics and physiology in the animal industry.

In 2017, she graduated with a bachelor's degree in animal science from NCSU and decided to continue her education at NCSU under Dr. Mark Knauer.

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INTRODUCTION

Piglet survival is an area of concern for pig farmers throughout the world as the topic is heavily related to both animal well-being and farm profitability. In order to enhance piglet performance and survival, the number and accessibility of functional teats on a sow is essential. Historical genetic selection of swine has focused on improving litter sizes, enhancing growth rate and reducing backfat thickness. However, these traits may have undesirable associations with other characteristics of interest (Balzani et al., 2016c). For instance, selection for increased litter size has decreased average piglet birth weight and increased sibling competition, resulting in reduced functional teat accessibility and piglet survival (Alexopoulos et al., 2018).

Although the number of functional teats has increased due to inclusion of total teat number in breeding goals, there has also been an increase in non-functional teat number (Lundeheim et al., 2013). Modern litter sizes commonly exceed the number of functional teats available, affecting the ability of newborn piglets to find a teat and suckle (Ocepek et al., 2016). This increases the risk of piglets being unable to achieve sufficient colostrum intake within the first 24 hours after birth, which is a rudimentary cause for decreased piglet weaning weight and the majority of piglet deaths that occur early postpartum (Quesnel et al., 2012). Sows with high functional teat number tend to have bigger litters and heavier piglet weight at weaning when compared to sows with fewer functional teats (Balzani et al., 2016a). In order to facilitate teat accessibility, knowledge of the genetics behind functional teat number is of fundamental importance to enhance sow's nursing abilities and improve piglet survival and performance.

REPLACEMENT GILT SELECTION CRITERIA

Phenotypic selection in swine for traits that increase piglet survival and productivity is especially important when selecting replacement gilts for a breeding herd. When purchasing or producing replacement gilts, the goal is to identify females that will be productive and remain in the breeding herd for at least three to four parities. Phenotypic traits that should be evaluated in replacement gilts include external maternal traits, including udder morphology and teat quality, and feet and leg soundness (Stalder et al., 2010).

Teat number is a commonly used measure for evaluating replacement gilt underline quality. Typically, selecting gilts with at least seven functional teats on each side of the underline that are adequately spaced and positioned is desired. This allows piglets to nurse uninhibited and acquire the nutrition required for survival. If demand for gilts is high at the time of gilt selection, the criteria for teat number might be overlooked (Wiegert & Knauer, 2018).

Evaluating teat quality is another important measure of underline characteristics that helps determine the overall number of functional teats. When the teat sphincter is unable to be seen at eye level, the teat is prone to remain inverted and non-functional (Muirhead & Alexander, 1997). Some inverted teats do become more normal and functional after the development of the mammary gland, but this is not guaranteed. Hence producers typically do not credit inverted teats when selecting for replacement gilts (Muirhead & Alexander, 1997).

UDDER CHARACTERISTICS

Modern sows tend to have larger body size and poor udder conformation that negatively affects the ability of newborn piglets to find a teat and suckle. Accessibility of teats decreases as sow parity advances. As sows continue to grow, teats become a greater distance from the floor or are less well exposed (Balzani et al., 2016a). Therefore, proper teat position on the underline and adequate space between the teats is crucial to reduce sibling competition and increase teat availability for suckling.

The Balzani research group (Balzani et al., 2016a,b,c,d) focused on four measurements of udder morphology in their studies; teat length, teat diameter, inter-teat distance within the same row, and teat distance from the abdominal midline. According to Balzani et al. (2016a), the largest proportion of variation in teat traits was at the sow level and can be explained by parity number, breed, and/or anatomical characterization (LEN = 51.3%; DIA = 40.6%). Variation in teat distance from the abdominal midline was highest at the teat pair position level (AML = 37.1%) and 35.4% of the variance in inter-teat distance was explained by sow and teat pair position interaction (Balzani et al., 2016a). Balzani et al. (2016c) found that middle teat pairs tended to be more perpendicular to the udder and have a larger teat diameter. Both anterior and middle teats had greater teat length, whereas anterior and posterior teats had shorter distance between the teat and abdominal midline (Balzani et al., 2016c). Anterior teats tended to not be perpendicular to the udder and contained about 29.7% of the non-functional teats that were recorded. The sixth and seventh posterior teats contained around 16.2% of non-functional teats recorded, whereas the rest of the teats on the udder contained less than 8.5% of the non-functional teats. (Balzani et al., 2016c)

Balzani et al. (2016d) reported heritability estimates for crossbreed Large White and Meishan sows. The authors reported heritability estimates for female reproductive traits were fairly low, 0.03 to 0.10, while udder morphology traits had greater heritability estimates of 0.22 to 0.53. Both positive and negative genetic correlations were found between udder traits and with reproductive traits. There was a positive genetic correlation between SAMER and reproductive traits (total number of piglets born and number born alive), yet an associated negative genetic correlation between these two traits and total teat number (0.89 and 0.69 vs. -0.46 and -0.47, respectively) (Balzani et al., 2016d). The number of liveborn piglets that died before ten days of age had a positive genetic correlation with teat diameter, inter-teat distance, and udder development, but was negatively correlated with total teat number (0.45, 0.87 and 0.46 vs. -0.57, respectively) (Balzani et al., 2016d). These results suggest that increasing udder size impairs teat access and impacts piglet mortality.

When comparing multiparous sows to primiparous sows there are many differences in udder morphology and teat quality. Sows in their first parity tend to have poorly developed udders and individual mammary glands that are not clearly defined when compared to multiparous sows (Balzani et al., 2016c). Multiparous sows have a greater mean teat pair distance, longer teat length, and larger teat diameter in comparison to primiparous sows (Ocepek et al., 2016). Vasdal and Andersen (2012) found that first and second parity sows on average had 46.5% of all functional teats available suckled by piglets during lactation. This percentage was reduced in older sows to an average of 41%, with fewer piglets suckling the row of teats closest to the floor as parity increased (Vasdal & Andersen, 2012). Piglets from older, multiparous sows took longer to suckle after birth and had a lower weight gain in the first 24 hours of life when compared to piglets from young parity sows (Vasdal & Andersen, 2012).

While a sow is lactating, there is an increase in the number of non-functional teats from the anterior and posterior portions of the udder. According to Ocepek et al. (2016), the increase is due to the positive relationship between the proportion of teats not suckled on the first day after birth and the number of teats that become non-functional by day 35 postpartum. As litter size increases, more piglets will suckle the lower teat row, but these piglets tend to gain less weight the first 24 hours after birth (Vasdal & Andersen, 2012). Teats that were not being suckled postpartum, due to compromised accessibility, were those with a greater distance between teat pairs on the first day after birth. For example, distance between lower middle teat pairs may exceed 16 centimeters (Ocepek et al., 2016). More than 80% of the teats that were becoming non-functional were in the middle and posterior positions of the udder (Ocepek et al., 2016). Increased teat pair distance in the middle and posterior udder portions causes difficulties for piglets to utilize teats because the teats in the upper row are too high and the teats in the lower row have reduced exposure. If teats are not used shortly after birth, the probability they will become non-functional during the lactation period is increased. Therefore, teat pair distance is an important characteristic for preserving teat function.

Balzani et al. (2016b) reported newborn piglets exhibiting a preference for teats found in the anterior and posterior portions of the udder. Perhaps this makes sense as teats closer to the abdominal midline have a greater inter-teat distance, making it more challenging for piglets to nurse. According to Balzani et al. (2016b), 41% of piglets chose to first suckle posterior teats, 33% of piglets chose anterior teats, and 27% of piglets chose the middle teats. It is clear that udder morphology greatly influences the success of piglets quickly finding a teat to suckle and acquire much needed colostrum.

TOTAL TEAT NUMBER

The improvement of total teat number will most likely be a valuable aid in improving sow productivity through increasing milk production, with the assumption that all teats produce the same amount of milk (Towers et al., 2016). Phenotypic expression of total teat number is limited to a few whole numbers, but there are many possible genotypic values. According to various research (Borchers et al., 2002; Clayton et al., 1981; Krupa et al., 2016; Lundeheim et al., 2013) reported means for total teat number is approximately 14 within a swine population, with some asymmetry in the number of teats that exist between the right and left sides of the underline (Willham & Whatley, 1963). Reported heritability estimates for total teat number across various research articles has been calculated to range between 0.07 and 0.42 (Towers, 2016). These heritability estimates indicate that a response to genetic selection for total teat number is a realistic expectation.

In a three-generation crossbreeding experiment mating Pietrain boars with Landrace, Large White, and Landrace × Large White crossbred sows the mean and standard deviation of total teat number in the F_1 generation was 14.1 and 0.9, respectively (Borchers et al., 2002). The F_2 generation total teat number had a mean of 13.8 and standard deviation of 1.0 (Borchers et al., 2002). Even though most of the F_2 animals had 14 total teats, similar to the F_1 animals, the mean and standard deviation reveals a tendency towards a reduced total teat number and perhaps higher variation. Borchers et al. (2002) also found that unequal teat number on each side of the body was observed in 29.3% of the F_1 animals and 38.9% of the F_2 animals, but the estimated heritability for asymmetry in left and right-side teat number was near zero.

The total number of teats in a population of Large White and Landrace pigs was observed near the mean (14 teats) with most of the population (86%) falling within one standard deviation of this mean (Clayton et al., 1981). The same study reported heritability for total teat number in males and females ranged from 0.13 to 0.24. There were no difference in heritability between sexes, but there was a significant difference in heritability between breeds observed (Clayton et al., 1981). Paternal half-sib heritability for teat number was found to be 0.32, which was less than the full-sib estimate of heritability in the same study, indicating a significant maternal effect on teat number (Pumfrey et al., 1980). Estimates for heritability within Oklahoma inbred and crossbred swine lines showed that heritabilities up to 0.40 for teat number per side. Differences in variance component estimates were found between males and females, with females boasting a larger variance component of 0.045 compared to 0.031 in males (Willham & Whatley, 1963). This is likely due to a maternal effect because the difference in variance components was equal to the genetic maternal variance and covariance of 0.014 reported in the same study. The additive genetic variance for teat number per side accounted for 28% of the total phenotypic variance estimated (Willham & Whatley, 1963).

In a study with three purebred populations and three crossbred populations represented, heritability estimates for total teat number ranged from 0.20 to 0.47 (McKay & Rahnefeld, 1990). The same study reported heritability for the number of posterior teats ranged from 0.08 to 0.39 and heritability of the number of anterior teats ranged from 0.03 to 0.21. Based on the genetic and phenotypic correlations between total teat number with posterior teat numbers and anterior teat numbers, selection for increased number of total teats would increase the number of both anterior and posterior teats (McKay & Rahnefeld, 1990). Though, there would be a greater increase in posterior teat number than anterior teat number due to the larger genetic correlations between posterior and total teat numbers (0.78-0.95) relative to anterior and total teat numbers (0.56-0.81).

Factors effecting total teat number in gilts was discovered to be the number of teats on the sow and the number of males in the litter (Drickamer et al., 1999). The same study evaluated other factors including: body mass at birth and weaning, litter size, number of teats on the boar, etc. A greater number of teats on the dam and a lower proportion of males in the litter in this study resulted in a greater number of teats on the gilt, thus helping confirm that the total number of teats on gilts is an outcome of inheritance from the dam. Taken together, these results suggest that teat number in female pigs is influenced by the number of teats on the dam and the proportion of males in the litter.

For teat number in Duroc boars' narrow sense heritability estimates ranged from 0.346 to 0.350 and dominance variance estimates were near 0.035 (Tan et al., 2017). These differences in variance estimates suggest that teat number is strongly regulated by an additive genetic component due to the estimate for narrow sense heritability. Genome-wide association studies (GWAS) can identify SNP's that are contributing to the variation in total number of teats in swine. Tan et al. (2017) reported SNP's on chromosomes 1, 6, 7, 10, 11, 12, and 14 accounted for 28% of the genomic heritability and 36% of the accuracy of prediction. According to Hirooka et al. (2001) there is evidence, in data from F_2 individuals from a cross between Meishan and Dutch pig lines, for quantitative trait loci (QTL) for teat number on chromosomes 2, 10, and 12, where the QTL on chromosomes 2 and 12 were imprinted. Due to the additive nature of the QTL on chromosome 10 the animals that inherited two Meishan alleles at this locus had 0.70 more teats than those that inherited both alleles from the Dutch lines (Hirooka et al., 2001).

Borchers et al. (2002) studied Landrace, Large White, and Pietrain crosses and found total teat number had a significant effect on growth development during pregnancy and carcass fatness traits. In contrast, a study on total teat number in Czech Landrace and Large White pigs showed no significant genetic correlations between total teat number with lean meat content, average daily gain, total number of piglets born per litter, and number of piglets weaned per litter (Krupa et al., 2016). The same study reported genetic correlations between total teat number with production and reproduction traits of -0.096 to 0.080. Given the findings of Krupa et al. (2016), total number of teats could be incorporated into routine genetic evaluation as a single or multitrait component as it appears to have an inconsequential influence on other production and reproduction traits.

FUNCTIONAL TEATS

At the time of selection some of the teats found on young gilts are believed to be less functional than others, due to the inability of the related mammary gland to produce enough milk or the teat to be suckled by piglets (Chalkias et al., 2013). Functional teats are teats that have a well-developed and predominant sphincter, and successfully produce enough milk to rear a piglet. Non-functional teats produce a reduced amount of milk that limits the sow rearing ability and includes inverted teats (teat that is turned inward to form a crater) and supernumerary teats (teat that is small and shorter in size compared to normal teats) (Towers, 2016). Inverted teats make the sow susceptible to mastitis and should be avoided. Teats can be classified functional and non-functional upon visual inspection during processing two to three days postpartum, but this differentiation between teats is not always accurate. Perhaps a more accurate determination of determining teat functionality would be to manipulate a teat at the time of farrowing to ensure production of milk (Alexopoulos et al., 2018).

Wiegert and Knauer (2018) reported that a one functional teat increase in sows improved piglet survival by 3.25% and tended to increase the number piglets weaned by 0.34. The results of this study suggest that selecting sows and gilts with increased number of functional teats can enhance piglet performance and survivability. According to Lundeheim et al. (2013) who studied a population of Yorkshire pigs, functional teat number averaged 14.2 and non-functional teats averaged 0.3. In this population 67% of pigs had zero non-functional teats, 7% of pigs had one non-functional teat, and 3% of pigs had two non-functional teats. The same study reported heritability estimates for functional and total teat number of 0.31 and 0.39, respectively, while non-functional teat number had a heritability estimate of 0.09. Functional and non-functional teat number were negatively correlated with one another yet had a positive correlation with total teat number (Lundeheim et al., 2013).

Marois and Larochelle (2008) evaluated total teat number, functional teat number, inverted teat number and supernumerary teat number using 173,466 Landrace pigs born between 1991 and 2006. The current study reported heritability estimates for total and functional teats of 0.38 and 0.30, respectively. Functional teat number had a positive genetic correlation with total teat number of 0.83, similar to the genetic correlation of 0.82 calculated by Lundeheim et al. (2013). Inverted teat number and supernumerary teat number also had positive genetic correlations with total teat number of 0.04 and 0.57, respectively. Marois and Larochelle (2008) reported an improvement of 0.26 functional teats achieved over five years (2002-2006). This is not surprising according to their reported heritability estimate of 0.30 and positive genetic correlation of 0.83 between total teat number and functional teat number.

Chalkias et al. (2013) studied the number of functional, non-functional, and total teats at three weeks of age and at 100 kilograms (kg) in Yorkshire pigs. The results revealed that males had three times more functional teats at 100 kg compared to females. Heritability estimates for functional teats were near 0.40 for both males and females at three weeks and 100 kg while heritability estimates for non-functional teats were generally low except for females at 100 kg (0.3). Genetic correlations between functional and non-functional teats for males and females at three weeks of age were 0.99 and 1.00, respectively, and at 100 kg were 0.84 and 0.72, respectively. The genetic correlation between functional and non-functional teats at 100 kg for females was -0.69, but these traits for males at 100 kg had a low positive genetic correlation of 0.18 (Chalkias et al., 2013). This difference between sexes at 100 kg could be because of low male variance due to gilts being recorded more often. It is also interesting to note that they observed 0.08 fewer non-functional teats in females born into smaller litters, which was significantly different than females from larger litters (Chalkias et al., 2013).

Clayton et al. (1981) reported the heritability of teat inversion was 0.20. Of the gilts utilized in that study, 17% were observed to have severely inverted teats. These affected gilts had a mean number of 4.01 inverted teats in comparison to the population mean of 0.738 teat inversions. Inverted teats were not distributed at random, but occurred most frequently in the anterior and middle portions of the udder. Of gilts with teat inversions, 97% of all affected pigs had one or more inverted teat in the anterior and middle udder portions (Clayton et al., 1981).

Balzani et al. (2016d) showed a positive genetic correlation between total teat number and non-functional teat number of 0.4. This suggests selection for increased number of total teats would also increase the number of non-functional teats. The same authors reported a negative genetic correlation between the number of non-functional teats with litter weight at ten days postpartum (-0.51). These results imply that sows with an increased number of non-functional teats inhibit the ability of offspring to suckle and thrive during lactation.

As a piglet nurses and suckles a functional teat, the milk ejection tends to last only 10 to 20 seconds approximately once per hour (Chalkias et al., 2013). This requires that each piglet has access to its own teat. As mentioned earlier, piglets tend to express a preference for teats in the anterior and posterior portions of the udder. Due to this preference, there are some teats that do not get suckled immediately after birth. According to Ocepek et al. (2016), the proportion of functional teats that are not used is not affected by parity. The same authors showed the proportion of functional teats that are not used significantly decreases during the lactation period from 21.4% on day one to 4.7% of functional teats not being used by day 35. However, there was a significant increase in the number of non-functional teats during lactation from 3.4% on day one to 21.5% by day 35 (Ocepek et al., 2016).

PIGLET PERFORMANCE AND SURVIVABILITY

Colostrum intake is one of the most important factors impacting piglet survival. For piglets that receive greater than 200 grams (g) of colostrum there was a 7.1% mortality rate in comparison to piglets that received less than 200 g and had a mortality rate of 43% (Alexopoulos et al., 2018). There is a low survival rate for piglets that have a birth weight of less than 0.9 kg and ingest less than 1,000 mg/dl of immunoglobulin G (IgG) serum concentration when compared to larger siblings (Cabrera et al., 2012). Low and average piglet birth weights tend to have higher pre-weaning mortality, but are able to overcome this if their colostrum intake totals at least 200 g and 250 g. Hence, intake of adequate amounts of colostrum is essential to improving piglet survival.

Consumption of more than 290 g of colostrum showed an increase of around two kg in weight at six weeks postpartum compared to piglets ingesting less than 290 g (Alexopoulos et al., 2018). This suggests that there is both improved growth and high weaning weights in piglets that receive higher quantities of colostrum. Nonetheless, colostrum intake is dependent on a piglets' ability to reach a teat to suckle. Hence piglet viability is an important factor explaining variability in colostrum consumption between piglets.

Quesnel et al. (2012) recommend a range of 200 g to 250 g of colostrum ingested per piglet within the first 24 hours postpartum to significantly reduce the risk of pre-weaning mortality, provide passive immunity from sow to piglet and allow for a slight weight gain. The same study reported at least one third of sows do not produce enough colostrum to fulfill their litter needs when following the above recommendation. Sow colostrum yield is not highly correlated with litter size or litter weight. Hence in genetic lines where litter sizes tend to be equal or greater than the number of teats available, the sow is unable to adapt her colostrum production to fill the needs of the entire litter. This inability to produce adequate colostrum results in higher sibling competition, increased pre-weaning mortality, and decreased piglet weight gain (Quesnel et al., 2012).

Cabrera et al. (2012) reported that sow parity had a significant effect on colostral IgG concentration. The same study reported a parity effect as IgG concentration in multiparous sows was 5% higher than primiparous sows. Even though greater IgG concentration is associated with older parity sows, both piglet survival and litter weaning weight decline after a sow reaches her third or fourth parity (Cabrera et al., 2012). This is because older sows have reduced teat accessibility, udder damage, and increased chance of disease that reduces milk production. Multiparous sows are also more prone to lameness which increases the risk of piglets getting crushed. Collectively these factors associated with greater parity sows result in higher pre-weaning mortality rates. Alexopoulos et al. (2018) showed that when there is less than one functional teat available per piglet the mortality rate is above 14%, but when more than one functional teat was available piglet mortality rate was below 8%. Thus, a minimum of one functional teat should be allotted to each individual piglet in a litter.

GENETIC ANALYSIS

For the studies discussed, estimation of variance components were performed to analyze the quantitative data collected. This approach to genetic data analysis is useful for further understanding the underlying genetics of teat and udder traits in pigs. Descriptive statistics gives researchers an idea of what to expect from more in-depth data analysis. Nick (2007) states that the first step to describing multivariate data is through simple descriptive statistics, such as frequency, mean, proportion, range, and distribution, which can then be displayed visually through various plots.

Variance component estimation is more complicated than descriptive statistics and requires statistical models and software programs. de Resende (2016) describes the restricted maximum likelihood/best linear unbiased predictor (REML/BLUP) program as one such procedure ideal for genetic evaluations. This program deals with imbalances in data, allows for comparison of individuals over time and space, corrects for environmental effects, and deals with complex data structures, leading to more accurate estimation of genetic parameters (de Resende, 2016). The BLUP program enhances selective accuracy for additive genetic effects, dominance effects, and genetic effects (de Resende, 2016).

To estimate variance and covariance components for traits of interest mixed linear animal models are commonly used. Zhang et al. (2011) utilized REML to obtain variance and covariance estimates, then with the BLUP method they estimated heritability and breeding value with their REML estimates. Lukac (2016) compared variance component estimates using different animal models to determine the best mixed model fit to estimate genetic parameters for production traits in his study utilizing Landrace, Yorkshire, and Landrace × Yorkshire gilts. The current study conducted this analysis using REML based on an animal model using the Wombat program with multivariate analyses (Lukac, 2016). This allowed the author to determine the significance of individual fixed effects, such as farm, year, season and breed, and their inclusion in various multivariate models, with individual animal influence incorporated as a random effect (Lukac, 2016).

Stratz et al. (2016) conducted pairwise bivariate analyses in their study on crossbred sows to calculate correlations of estimated genetic parameters. The current study utilized univariate linear mixed models for each observed trait to estimate heritability of that trait. The authors also decided to combine sows with parities greater than or equal to four when conducting their analyses to create parity groups containing similar number of sows (Stratz et al., 2016). This advantageous due to the number of sows in each parity decreasing significantly as parity increases.

Paternal half-sib and full-sib analyses can also be used to estimate components of variance and covariance, heritabilities, and genotypic and phenotypic correlations for teat traits. Pumfrey (1980) applied this approach when studying the inheritance of teat number and its relationship to maternal traits in swine. Utilizing pedigreed sows, their model included effects for line-generation, sires within line-generation, dams within sires, and progeny within dams.

CONCLUSION

It is apparent that teat number, especially functional teat number, plays a significant role in piglet survival and performance when a sow has more piglets than teats available. Therefore, these traits should be included in breeding objectives to enhance optimal genetic improvement (Balzani et al., 2016d). Continued genetic selection for larger litter sizes will be futile without the selection for traits that enhance litter quality, such as increased total and functional teat number. With the existence of sufficient genetic variation for teat traits, genetic gains for total and functional teat number are achievable (Marois & Larochelle, 2008).

Typically, the total number of teats observed on replacement gilts represent their maternal potential (Krupa et al., 2016). Hence selecting gilts based on the number of functional teats, while avoiding selecting pigs with inverted or other non-functional teats is a reasonable approach for improving teat quality. Besides teat functionality, udder morphology can influence the success of piglets quickly finding a teat and suckling (Balzani et al., 2016b). Teat distance from the abdominal midline and inter-teat distance are two important udder characteristics that can significantly affect teat use and availability (Ocepek et al., 2016).

Understanding the genetics behind functional teats in swine and including these traits in genetic selection will help decrease sibling competition for teat accessibility and improve sow maternal ability (Krupa et al., 2016). This will then in turn have a positive impact on piglet survival and performance through improved teat accessibility to piglets postpartum. Increasing the ability of piglets to suckle will also increase colostrum intake within the first 24 hours after birth, leading to improved pre-weaning mortality rates, increased growth and development, and improved passive immunity protection between the sow and piglet.

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CHAPTER 2

THE GENETICS OF FUNCTIONAL TEATS IN SWINE

ABSTRACT

The objective of this study was to evaluate the genetics of functional teat number in swine. Piglet survival is of great importance for swine producers throughout the world due to its relationship with animal well-being and farm profitability. Availability and accessibility of functional teats on a sow is essential for enhancing piglet livability. Teat traits including total teat number (TT), functional teat number (FT), and non-functional teat number (NFT), were observed and recorded on 3,099 Landrace × Large White F1 sows. Variance components were estimated using AIREMLF90. Models included parity, farm, individual scorer, and phase of production as fixed effects. Means for TT, FT and NFT at farrowing were 14.93, 13.90 and 1.03, respectively, and 14.43, 13.02 and 1.15, respectively, at weaning. For farrowing, weaning and combined datasets, TT means were greater ($P<0.01$) than FT means. Heritability estimates for TT, FT and NFT ranged from 0.18 to 0.37, 0.16 to 0.28, and 0.14 to 0.18, respectively. Total teat number and functional teat number had positive genetic correlation estimates across farrowing and weaning datasets ranging from 0.68 to 0.77. Functional mammary glands had genetic correlation estimates of 0.72 and -0.57 with FT and NFT, respectively. At farrowing the genetic correlation estimate between NW and FT was positive (0.50), whereas the genetic correlation estimate between NW and NFT was negative (-0.38). An increase of one functional teat increased number of piglets weaned by 0.27. Sufficient genetic variation for total teat number and functional teat number was observed signifying that genetic improvement for these traits is possible. Results suggest that by focusing selection on functional teat number an increase in non-functional teat number can be avoided. Therefore, utilizing functional teat number in the breeding goal should improve general teat quality and sow performance. By increasing the

number of functional teats on a sow, producers can increase the number of piglets that survive to weaning and grow quickly.

INTRODUCTION

Piglet survival is a subject of great interest for pig producers worldwide due to its associations with animal well-being and farm profitability. Enhancing piglet performance and survival is dependent on both the number and accessibility of functional teats on a sow. Historic genetic selection of swine for increased litter sizes and improved finishing traits (i.e. growth rate, carcass lean content) have inadvertently increased selection for other undesirable traits (Balzani et al., 2016c). These undesirable traits have been shown to include reduced functional teat accessibility which is disadvantageous since the number of functional teats available per piglet is positively related to piglet survival (Alexopoulos et al., 2018).

Reduced teat functionality and accessibility increases the risk of newborn piglets failing to intake sufficient amounts of colostrum. Both teat functionality and colostrum intake is the rudimentary cause for decreased piglet weaning weight and the majority of early postpartum piglet deaths (Quesnel et al., 2012). A range of 200 g to 250 g of colostrum ingested per piglet within the first 24 hours postpartum is recommended to reduce the risk of pre-weaning mortality, provide passive immunity from sow to piglet and allow a slight weight gain (Quesnel et al., 2012). Long-term negative connotations, such as decreased piglet birth weight, increased sow body size and increased sibling competition, will continue with the genetic selection for increased litter sizes. Thus, including teat traits, particularly functional teat number, in the breeding objective would help alleviate these negative consequences (Balzani et al., 2016c).

Understanding the genetics of teat quality traits in swine and including these traits in genetic selection will help decrease sibling competition for teat accessibility and improve sow maternal ability (Krupa et al., 2016). Knowledge of the genetics behind functional teat number is of fundamental importance to facilitate teat availability and improve piglet survival and performance. Hence, the overall objective of this study was to evaluate the genetics of functional teats in swine.

MATERIALS AND METHODS

Animals and Teat Traits

Data (n=3,701sows) from Landrace × Large White F1 females (Smithfield Premium Genetics, Rose Hill, NC), within seven sow farms located in eastern North Carolina were used. Sows were housed in farrowing barns with a range of 10 to 30 standard farrowing stalls per room. Management at farms was not altered for this study, thus sows were not assisted during farrowing. Teat traits observed on all sows included total teat number (TT), functional teat number (FT), and non-functional teat number (NFT). For sows evaluated within three days prior to weaning, damaged teat number (DT) and functional mammary glands (FG) were also assessed. Teats were classified according to the scoring system (Figure 1) proposed by Muirhead and Alexander (1997) and descriptions from the article “Genetics of teat number in swine”. Functional teats were elongated teats that had a well-developed and predominant sphincter and NFT were classified as teats that were inverted (turned inward to form a crater) or supernumerary (small and shorter in size compared to normal teats) (Towers, 2016). Damaged teats were teats damaged during lactation by either excessive chewing by piglets or getting caught in the flooring. If at weaning mammary glands still appeared swollen with milk they were classified as FG. Total number of teats was calculated from the sum of FT, NFT and DT.

Data Collection

Sampling occurred biweekly between May 2018 and August 2018. Sows that appeared to have farrowed recently and sows within three days of weaning were assessed. Only a small proportion of sows were sampled at both farrowing and weaning. Data was collected during feeding to ensure that a majority of sows were standing while observed. If a sow was lying down it was not included in the study. When a sow is lying down there is an increased chance that the visibility of certain teats will be impaired, thus negatively affecting the accuracy in classifying teats. Sow farrow date, parity, and number of piglets born alive (NBA) were recorded. The number of piglets weaned (NW) for every sow sampled was recorded and obtained from the Smithfield Premium Genetics Pig Knows database.

Data Editing

Mac Terminal v. 2.8.2 and RStudio v. 1.1.463 was used to edit collected data. Data from 3,701 sows was available for analysis. Duplicate records and outliers for TT, were excluded from the analyses. Records where sows were not sampled within five days of farrowing or within three days prior to weaning were also excluded. Records missing a value for any of the observed traits were removed from analysis as well. After editing, data from 3,099 sows were retained for analysis. The number of records that originated from sows that just farrowed was 1,840, whereas the number of records originating from sows about to wean was 1,259. For all sows sampled there were a total of 300 unique sires, with 276 unique sires for sows sampled at farrowing and 235 unique sires for sows sampled at weaning.

Statistical Analysis

Descriptive statistics for each trait were calculated using RStudio v. 1.1.463. Genetic analyses utilized restricted maximum likelihood (REML) statistical models. Univariate and bivariate models were performed to estimate variance components for each trait: TT, FT, NFT, DT, FG, and NW. Pedigrees for sows sampled were provided by the Pig Knows database to be utilized in the data analysis for variance component estimation. Pedigrees included in the analysis went back five generations and comprised of both the dam and the sire of the parents of the sow sampled. The RENUMF90 v. 1.122 program (Misztal et al., 2016) processed the data by performing comprehensive pedigree checks and creating the proper parameter file for AIREMLF90 v. 1.135 (Misztal et al., 2016). The AIREMLF90 v. 1.135 program was applied to determine relationships between observed traits. Models included fixed effects of sow parity, farm, individual teat scorer, and phase of production, whereas individual animal was included as a random effect. Common litter and sire effects were excluded from model analysis due to resulting genetic variance estimates being essentially zero, indicating that the level of between group variability was not sufficient to warrant incorporating these effects in the model.

Heritability was calculated from the estimated variance components of the univariate models using the following equation:

$$(1)\ h^2 = \frac{a}{(a+e)}$$

where h^2 is the narrow-sense heritability, a is the additive genetic variance estimate, and e is the residual variance estimate. Standard errors for heritability estimates were calculated using the following equation:

$$(2)\ SE^2(h^2) = \begin{pmatrix} \frac{h^2(1-h^2)}{a} & -\frac{h^2(h^2)}{a} \end{pmatrix} \begin{pmatrix} var(a) & cov(a,e) \\ cov(e,a) & var(e) \end{pmatrix} \begin{pmatrix} \frac{h^2(1-h^2)}{a} \\ -\frac{h^2(h^2)}{a} \end{pmatrix}$$

where a is the additive genetic variance and e is the residual variance. The leading row vector and following column vector are partial derivatives solved by taking the partial derivative of h^2 with respect to a and e, respectively. Components of the internal matrix were taken from the inverse of the average information matrix output by AIREMLF90. Bivariate model analyses were conducted to estimate genetic covariances between combinations of the teat traits, with which genetic correlations where calculated using the following equation:

$$(3)\ r = \frac{x_{12}}{\sqrt{x_1 x_2}}$$

where r is the genetic correlation, x_{12} is the genetic covariance between traits 1 and 2, x_1 is the genetic variance of trait 1, and x_2 is the genetic variance of trait 2. Standard errors for genetic correlations estimates were calculated using the following equation:

$$(4)\ SE^2(r) = \begin{pmatrix} -\frac{r}{2x_1} & -\frac{r}{2x_2} & \frac{r}{x_{12}} \end{pmatrix} \begin{pmatrix} var(x_1) & cov(x_1, x_2) & cov(x_1, x_{12}) \\ cov(x_2, x_1) & var(x_2) & cov(x_2, x_{12}) \\ cov(x_{12}, x_1) & cov(x_{12}, x_2) & var(x_{12}) \end{pmatrix} \begin{pmatrix} -\frac{r}{2x_1} \\ -\frac{r}{2x_2} \\ \frac{r}{x_{12}} \end{pmatrix}$$

where r is the genetic correlation, x_{12} is the genetic covariance between traits 1 and 2, x_1 is the genetic variance of trait 1, and x_2 is the genetic variance of trait 2. Components for the matrix were also taken from the inverse of the average information matrix. Expected progeny differences (EPD) values for the sires of sows sampled were obtained from the AIREMLF90 v. 1.135 output.

RESULTS

Descriptive Statistics

Distributions of TT, FT, NFT and DT are shown in Figure 2. Only FT seems to be normally distributed, TT at first glance appears to be normally distributed, but the number of animals with a total teat number less than 14 is significantly lower. Distributions for NFT and DT were skewed to the right. Summary statistics for teat and production traits are shown in Table 1. Average number of TT was greater (P<0.01) at farrowing when compared to weaning (14.93 vs. 14.43). Similarly, average number of FT at farrowing was greater (P<0.01) than at weaning (13.90 vs. 13.02). Bar graphs give a visual representation of the difference in means for TT and FT at farrowing and weaning in Figure 3.

Average number of NFT was lower (P<0.01) at farrowing when compared to weaning (1.03 and 1.15, respectively). Damaged teats and FG were only observed on sows at weaning, therefore means for these traits were only calculated from the wean data. Damaged teats and FG had means of 0.26 and 9.67, respectively.

Farm and parity means for teat traits are shown in Table 2. Across all farms, TT, FT and NFT ranged from 14.45 to 14.91, 13.30 to 13.96, 0.58 to 1.29. For TT, Farm B had a higher (P<0.01) mean than Farms A, C, D, F, and G (14.91 vs. 14.68, 14.71, 14.59, 14.51 and 14.45, respectively). Farm G had a lower (P<0.05) mean than Farms B and E (14.45 vs. 14.91 and 14.81, respectively). For FT, Farm E had a higher (P<0.01) mean than Farms A, B, C, D and F (13.96 vs. 13.30, 13.62, 13.22, 13.69 and 13.60, respectively). Farms A and C had lower (P<0.05) FT than all other farms. For NFT, Farms A and C had greater (P<0.05) means than Farms B, D, E, F, and G (1.29 and 1.40 vs. 1.12, 0.79, 0.79, 0.77 and 0.58, respectively. Figures 4, 5, and 6 contain bar graphs illustrating the teat mean differences for TT, FT, and NFT, respectively, across the seven farms sampled.

Across parity groups, means for TT, FT and NFT ranged from 14.56 to 14.85, 13.43 to 13.69, 0.99 to 1.28, respectively. For TT, first parity sows had a fewer (P<0.05) teats when compared to all other parities (14.56 vs. 14.72, 14.85, 14.72, 14.77 and 14.82). First parity sows also had lower (P<0.05) FT when compared to second and third parity sows (13.43 vs. 13.61 and 13.69, respectively). For NFT, sows in a parity of six or greater had lower (P<0.001) than first, second, and third parity sows (1.28 vs. 1.00, 0.99 and 1.06, respectively). Figures 7, 8, and 9 contain bar graphs illustrating the teat mean differences for TT, FT, and NFT, respectively, across the parity groups.

Genetic Variance Components and Heritability

Genetic variance component estimates for teat traits are reported in Table 3. Total teat number had greater additive genetic variance at farrowing and FT additive genetic variance was greater at weaning (0.39 and 0.33, respectively). Genetic variances for the wean data were lower for TT when compared to the farrow dataset. The resulting heritability estimates for TT and FT from the wean data were lower compared to the farrow data. Even though the additive genetic variance for FT was higher for the wean data compared to the farrow data the heritability estimate for FT was lower for the wean data. Heritability estimates for TT, FT and NFT ranged between 0.18 and 0.37, 0.16 and 0.28, and 0.14 and 0.18, respectively. Heritability estimates for DT and FG from the wean data were 0.03 and 0.06, respectively.

The additive genetic variance and heritability estimate calculated for NW at farrowing was 0.31 and 0.11, respectively. For the wean and combined datasets the AIREMLF90 program was unable to converge when estimating the additive genetic variance for NW. Therefore, there are no values reported for NW under the Combined and Wean columns in Table 3.

Genetic Correlations

Genetic correlation estimates between teat traits are shown in Tables 4 and 5 for farrow data and wean data, respectively. The genetic correlation estimates between TT and FT for the farrow and wean datasets were both large (0.78 and 0.68, respectively). The farrow dataset had a greater positive genetic correlation estimate between TT and NFT when compared to the wean dataset (0.47 vs. 0.22, respectively). Whereas, the negative genetic correlation estimate between FT and NFT from the wean data was greater than the farrow data (-0.57 vs. -0.19, respectively).

The genetic correlation estimates between NW and TT and FT at farrowing were 0.25 and 0.50, respectively.

For the wean dataset the genetic correlation between NFT and DT was 0.04 (Table 6). Damaged teats had negative genetic correlations with TT and FT of -0.22 and -0.30, respectively. Total teat number and FG had a positive genetic correlation of 0.17. The genetic correlation estimate between FG and FT was 0.72, yet FG had negative genetic correlations with NFT and DT of -0.57 and -0.98, respectively. Also, for the wean dataset the AIREMLF90 program was unable to converge when estimating the additive genetic covariances between NW and other teat traits. Therefore, there are no genetic correlation estimates reported between NW and the other teat traits in Table 5.

Linear Regression of Number Weaned and Sire Expected Progeny Differences

According to the linear regression results relating the number of piglets weaned to total teat number and functional teat number, at farrowing an increase of one functional teat on a sow increases the number of piglets weaned by 0.27. Also at farrowing, an increase of one total teat on a sow increases the number of piglets weaned by 0.14. The linear regression estimates at weaning for total teat number and functional teat number were similar, where a one teat increase would increase the number of piglets weaned by 0.16 and 0.18, respectively. Linear regression results are shown in Table 6.

Table 7 shows the range of sire expected progeny differences (EPD) for each observed trait, TT, FT, NFT, and NW. For the teat traits, TT and FT had the greatest ranges of EPD values (-0.83 to 1.44 total teats and -1.39 to 1.14 functional teats). The EPD values for NFT ranged from -0.57 to 0.65 non-functional teats, while the NW sire EPD values ranged from -4.13 to 2.27 piglets weaned.

DISCUSSION

A major goal of pig production at the sow farm level is to produce piglets that survive to weaning and grow quickly, as well as sows that are able to stay in the herd and produce numerous consistent litters. Ensuring the presence of sufficient number of functional teats on the sow is one way to successfully increase piglet survivability and performance.

For the sample population 92% of the teats were classified functional, 7.3% non-functional, and 0.7% damaged. In agreement, Balzani et al. (2016b) and Balzani et al. (2016c) reported the percentage of functional teats ranged from 95.2% to 98% and non-functional teats ranged from 2% to 4.9%. While most teats are functional, the number of functional teats does not always exceed litter size in hyper prolific sows. Therefore, increasing FT to keep up with increasing litter sizes is essential. In the present study, calculated means for TT (14.43-14.93) were within the ranges reported in various literature (Marois & Larochelle, 2008; Krupa et al., 2016; Lundeheim et al., 2013). Borchers et al. (2002) reported means ranging from 13.8 to 14.1 for total teat number, whereas Krupa et al. (2016) reported means ranging from 14.61 to 14.89. The FT means calculated in the present study (13.02-13.90) was lower than the FT mean of 14.83 reported by Wiegert and Knauer (2018).

Modern litter sizes have been shown to frequently exceed the number of functional teats available, negatively affecting the piglets' ability to find a teat and suckle (Ocepek et al., 2016). It has been found that sows with higher functional teat number tend to have heavier piglet weight at weaning compared to sows with fewer functional teats (Balzani et al., 2016a). Thus, it is apparent that functional teat number has a significant impact on sow performance, especially when a sow has more piglets than available teats.

At weaning, mean FG was lower compared to the FT mean, perhaps indicating that not all functional teats are being utilized by piglets during lactation. These results are supported by Vasdal and Anderson (2012) who reported less than half of available functional sows teats were suckled by piglets, with the percentage of suckled teats decreasing as sow parity increased. In this study it is not known whether mammary glands became non-functional through lack of nursing or the cessation of milk production.

The mean of damaged teats recorded in the sample population was 0.26. However, these teats were most likely functional before becoming damaged due to environmental influences. According to Norring et al. (2006) sows with larger litters had more damaged teats at weaning than at farrowing. Damage could be due to an increase in the intensity of piglet nursing behavior or by increased ventral lying of the sow. The occurrence of damaged teats causes a previously functional teat to become necrotic and then non-functional.

The variation in FT explained by genetics was higher than the other teat traits, except for TT with the farrow dataset. Overall, the amount of variation of the teat traits explained by genetics was low to moderate, whereas the largest proportion of variation was associated with the residual, comparable to Balzani et al. (2016c). Thus, a majority of variance remained unexplained by the model.

Compared to the heritability estimates reported in the literature, estimates in the current study were generally within the literature ranges. Heritability estimates for FT ranged between 0.30 and 0.42 (Marois & Larochelle, 2008; Chalkias et al., 2013). For TT, the lowest heritability estimate reported in the literature was 0.23 by Borchers et al. (2002) and the highest estimate was 0.53 by Hirooka et al. (2001). These studies utilized both males and females in their analysis which could account for the differences in heritability estimates between this study and literature estimates. It is also possible that with a larger sample population the heritability estimates could be improved. The heritability estimates for NFT in the current study fell within the literature range of 0.02 to 0.29 (Chalkias et al., 2013). When comparing the heritability estimates from the wean data to the farrow data, the wean data had lower heritability estimates. This reduction in the estimates could be due to many environmental factors influencing the teat traits observed prior to weaning, such as damage to teats. Previous studies did not evaluate DT and FG, but the heritability estimates for these two traits was exceedingly low (0.03 and 0.06, respectively), indicating that these traits do not have a strong genetic component. The present results indicate that greater genetic variation can be found when evaluating teat traits at farrowing when compared to at weaning.

Genetic correlation estimates between TT and FT were large across datasets (0.68-0.78) and are comparable to the positive genetic correlation of 0.82 between TT and FT reported by Lundeheim et al. (2013). This indicates that as TT increases FT also increases. Lundeheim et al. (2013) also reported a positive correlation of 0.21 between TT and NFT and a negative correlation of -0.34 between FT and NFT. These findings are different from the results of this study with the exception of the genetic correlations between TT and NFT at weaning (0.22). Fpr the present study the genetic correlation between TT and NFT at farrowing was 0.47, which was higher than the correlation reported by Lundeheim et al. (2013). Also, the genetic correlations between FT and NFT for the present study were lower at farrowing (-0.19) and higher at weaning (-0.57) compared to estimates provided by Lundeheim et al. (2013). Balzani et al. (2016d) reported a moderate positive genetic correlation between TT and NFT of 0.40, which is higher than the correlation estimate for the wean dataset, but still indicates that increasing TT will also increase NFT. With FT and NFT being positively correlated with TT, but negatively correlated with each other can assume that these two traits are parts of the total.

In addition to teat functionality, sow udder morphology can influence the success of piglets in quickly finding a teat and suckling (Balzani et al., 2016b). Teat distance from the abdominal midline and inter-teat distance are two important udder characteristics that can significantly affect teat use and availability. Multiparous sows, compared to primiparous sows, have a greater mean teat pair distance, longer teat length, and larger teat diameter (Ocepek et al., 2016). This explains why piglets from high parity sows took longer to first suckle after birth and had a lower weight gain in the first 24 hours postpartum than piglets from low parity sows (Vasdal & Andersen, 2012).

The genetic correlations estimated between FG and FT, NFT and DT were large correlations compared to the other genetic correlations estimated from the wean data (0.72, -0.57 and -0.98, respectively). These results indicate that FG is greatly influenced by FT, NFT, and DT, which corresponds with the idea that for a mammary gland to be functional it must have an equivalent functional teat. Therefore, if FT increases then FG should also increase, but if NFT and DT increases then FG should decrease. Functional mammary gland can thus be a useful indicator of the number of functional teats being utilized by piglets during the lactation period. It is important to note that the standard errors calculated for the wean dataset genetic correlations were quite large, indicating that the sample size could have been too small.

It is obvious with previous literature that increasing the number of functional teats on a sow is essential for improving piglet survival to weaning. Krupa et al. (2016) reported in their study an average of 10.15 piglets weaned, which was similar to the average of piglets weaned in the present study (10.55-10.56). They also reported that NW had a small heritability of 0.07 and a residual variance of 0.88. Their heritability estimate was similar to the heritability estimate reported in the present study (0.11). The present study also had a much larger residual variance of 2.47 associated with NW at farrowing indicating that most of the variance is due to an environmental component rather than a genetic component. In the present study the genetic correlation estimate of 0.25 between TT and NW at farrowing was much larger than the genetic correlation of 0.08 reported by Krupa et al. (2016). The positive genetic correlation of 0.50 between NW and FT indicates that an increase in FT should result in an increase in NW, whereas, the negative genetic correlation of -0.38 between NW and NFT indicates an increase in NFT should decrease NW. These results are further supported by the linear regression results where having one more functional teat at farrowing increases the number of piglets weaned by 0.27 piglets.

CONCLUSION

It is apparent that teat number, especially functional teat number, plays a significant role on piglet survival and performance when a sow has more piglets than teats available. Continued genetic selection for larger litter sizes will be futile without the selection for traits that enhance litter quality, such as increased total and functional teat number. Understanding the genetics behind functional teats in swine and including these traits in genetic selection will have a positive impact on sow performance and piglet survival through improving teat accessibility to piglets postpartum. Increasing the ability of piglets to suckle will also increase colostrum intake within the first 24 hours after birth, leading to improved pre-weaning mortality rates, increased growth and development, and improved passive immunity protection between the sow and piglet.

Sufficient genetic variation for total teat number and functional teat number was identified, signifying that improvement for teat traits is possible. Yet breeders should use caution when including total teat number in the breeding goal as it had a positive correlation with non-functional teat number. Hence, breeders should target functional teat number. With previous studies also indicating that increased functional teat number has a positive impact on piglet colostrum intake and survivability selection of females with a greater number of functional teats should be emphasized. Utilizing functional teat number in breeding goals, while also avoiding selecting pigs with inverted or extra teats, should improve the general quality of teats and sow performance. By increasing the number of functional teats on a sow, producers can increase the number of piglets that survive to weaning and grow quickly, which is one of their primary goals.

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Table 1. Descriptive statistics of teat traits, number born alive, and number weaned included in the analysis for combined data, farrow data, and wean data. TT = total number of teats, FT = functional teat number, NFT = non-functional teat number, DT = damaged teat number, FG = number of functional mammary glands, and NW = number weaned.

	Combined		**Farrow**		**Wean**	
	Mean ± SE	SD	Mean ± SE	SD	Mean ± SE	SD
TT	14.72 ± 0.022^{a}	1.23	14.93 ± 0.028^{b}	1.23	14.43 ± 0.033^{c}	1.16
FT	13.54 ± 0.025^{a}	1.42	13.90 ± 0.087^{b}	1.20	13.02 ± 0.044^{c}	1.55
NFT	1.08 ± 0.021^{a,b}	1.16	1.03 ± 0.027^{a}	1.16	1.15 ± 0.034^{b}	1.20
DT	-	-	-	-	0.26 ± 0.016	0.56
FG	-	-	-	-	9.67 ± 0.045	1.59
NW	10.55 ± 0.031	1.76	10.55 ± 0.041	1.77	10.56 ± 0.049	1.74

^{a,b,c} indicate statistical significance ($P<0.01$) of the difference between means for teat traits and type of data analyzed.

Table 2. Descriptive statistics of teat traits grouped by farm and parity utilizing combined data. TT = total number of teats, FT = functional teat number, NFT = non-functional teat number. TT = total number of teats, FT = functional teat number, NFT = non-functional teat number, DT = damaged teat number, FG = number of functional mammary glands, and NW = number weaned.

		TT		**FT**		**NFT**		
		Mean	SD	Mean	SD	Mean	SD	N
Farm	A	14.68^{b,c}	1.20	13.30^{a}	1.44	1.29^{d}	1.22	669
	B	14.91^{d}	1.29	13.62^{b}	1.43	1.12^{c}	1.21	660
	C	14.71^{b,c}	1.25	13.22^{a}	1.48	1.40^{d}	1.28	607
	D	14.59^{a,b}	1.18	13.69^{b}	1.35	0.79^{b}	0.95	486
	E	14.81^{c,d}	1.27	13.96^{c}	1.27	0.79^{a,b}	1.02	458
	F	14.51^{a,b}	1.23	13.60^{b}	1.36	0.77^{a,b}	1.00	124
	G	14.45^{a}	0.97	13.78^{b,c}	1.09	0.58^{a}	0.94	95
Parity	1	14.56^{a}	1.23	13.43^{a}	1.46	1.00^{a}	1.13	737
	2	14.72^{b}	1.21	13.61^{b,c}	1.34	0.99^{a}	1.17	569
	3	14.85^{b}	1.21	13.69^{c}	1.37	1.06^{a,b}	1.17	595
	4	14.72^{b}	1.19	13.49^{a,b}	1.52	1.14^{b,c}	1.22	470
	5	14.77^{b}	1.31	13.55^{a,b,c}	1.42	1.13^{a,b,c}	1.21	327
	6+	14.82^{b}	1.26	13.47^{a,b}	1.38	1.28^{c}	1.20	401

^{a,b,c,d} indicate statistical significance ($P<0.05$) of the difference of teat trait means between farms or sow parities.

Table 3. Variance and heritability estimates for teat traits (*SE within brackets*). TT = total number of teats, FT = functional teat number, NFT = non-functional teat number, DT = damaged teat number, FG = number of functional mammary glands, and NW = number weaned.

	Combined			**Farrow**			**Wean**		
	σ_A^2	σ_R^2	h^2	σ_A^2	σ_R^2	h^2	σ_A^2	σ_R^2	h^2
TT	0.53 (*0.07*)	0.92 (*0.06*)	0.37 (*0.003*)	0.39 (*0.10*)	1.11 (*0.09*)	0.26 (*0.006*)	0.23 (*0.11*)	1.11 (*0.11*)	0.18 (*0.009*)
FT	0.48 (*0.08*)	1.22 (*0.07*)	0.28 (*0.006*)	0.31 (*0.09*)	1.13 (*0.08*)	0.22 (*0.005*)	0.33 (*0.15*)	1.67 (*0.15*)	0.16 (*0.011*)
NFT	0.18 (*0.05*)	1.10 (*0.05*)	0.14 (*0.002*)	0.15 (*0.07*)	1.16 (*0.08*)	0.12 (*0.004*)	0.18 (*0.09*)	1.00 (*0.09*)	0.15 (*0.007*)
NW	-	-	-	0.31 (*0.15*)	2.47 (*0.16*)	0.11 (*0.008*)	-	-	-
DT	-	-	-	-	-	-	0.008 (*0.02*)	0.30 (*0.02*)	0.03 (*0.001*)
FG	-	-	-	-	-	-	0.14 (*0.15*)	2.28 (*0.17*)	0.06 (*0.01*)

Table 4. Estimates of genetic covariance (above the line) and genetic correlations (below the line) between observed traits from the farrow data (*SE within brackets*). TT = total number of teats, FT = functional teat number, NFT = non-functional teat number, and NW = number weaned.

Teat Traits	TT	FT	NFT	NW
TT	-	0.26 (*0.08*)	0.11 (*0.07*)	0.09 (*0.09*)
FT	0.78 (*0.05*)	-	-0.04 (*0.06*)	0.15 (*0.09*)
NFT	0.47 (*0.12*)	-0.19 (*0.12*)	-	-0.08 (*0.07*)
NW	0.25 (*0.07*)	0.50 (*0.08*)	-0.38 (*0.14*)	-

Table 5. Estimates of genetic covariance (above the line) and genetic correlations (below the line) between observed traits from the wean data (*SE within brackets*). TT = total number of teats, FT = functional teat number, NFT = non-functional teat number, DT = damaged teat number, and FG = number of functional mammary glands.

Teat Traits	TT	FT	NFT	DT	FG
TT	-	0.19 (*0.10*)	0.04 (*0.08*)	-0.009 (*0.03*)	0.03 (*0.09*)
FT	0.68 (*0.06*)	-	-0.14 (*0.09*)	-0.02 (*0.04*)	0.15 (*0.11*)
NFT	0.22 (*0.25*)	-0.57 (*0.26*)	-	0.001 (*0.03*)	-0.09 (*0.09*)
DT	-0.22 (*6.60*)	-0.30 (*0.40*)	0.04 (*0.20*)	-	-0.04 (*0.03*)
FG	0.17 (*0.34*)	0.72 (*0.50*)	-0.57 (*1.01*)	-0.98 (*8.71*)	-

Table 6. Results from linear regression showing the relationship of number of piglets weaned with total teat number and functional teat number.

	Total teat number		**Functional teat number**	
	Farrow	Wean	Farrow	Wean
Estimate ± SE	0.14 ± 0.03	0.16 ± 0.04	0.27 ± 0.03	0.18 ± 0.03

Table 7. Range of Expected Progeny Differences (EPD) for observed traits on sires of sows sampled. TT = total number of teats, FT = functional teat number, NFT = non-functional teat number, NW = number weaned

	Trait			
	TT	FT	NFT	NW
Range of EPD	-0.83-1.44	-1.39-1.14	-0.57-0.65	-4.13-2.27

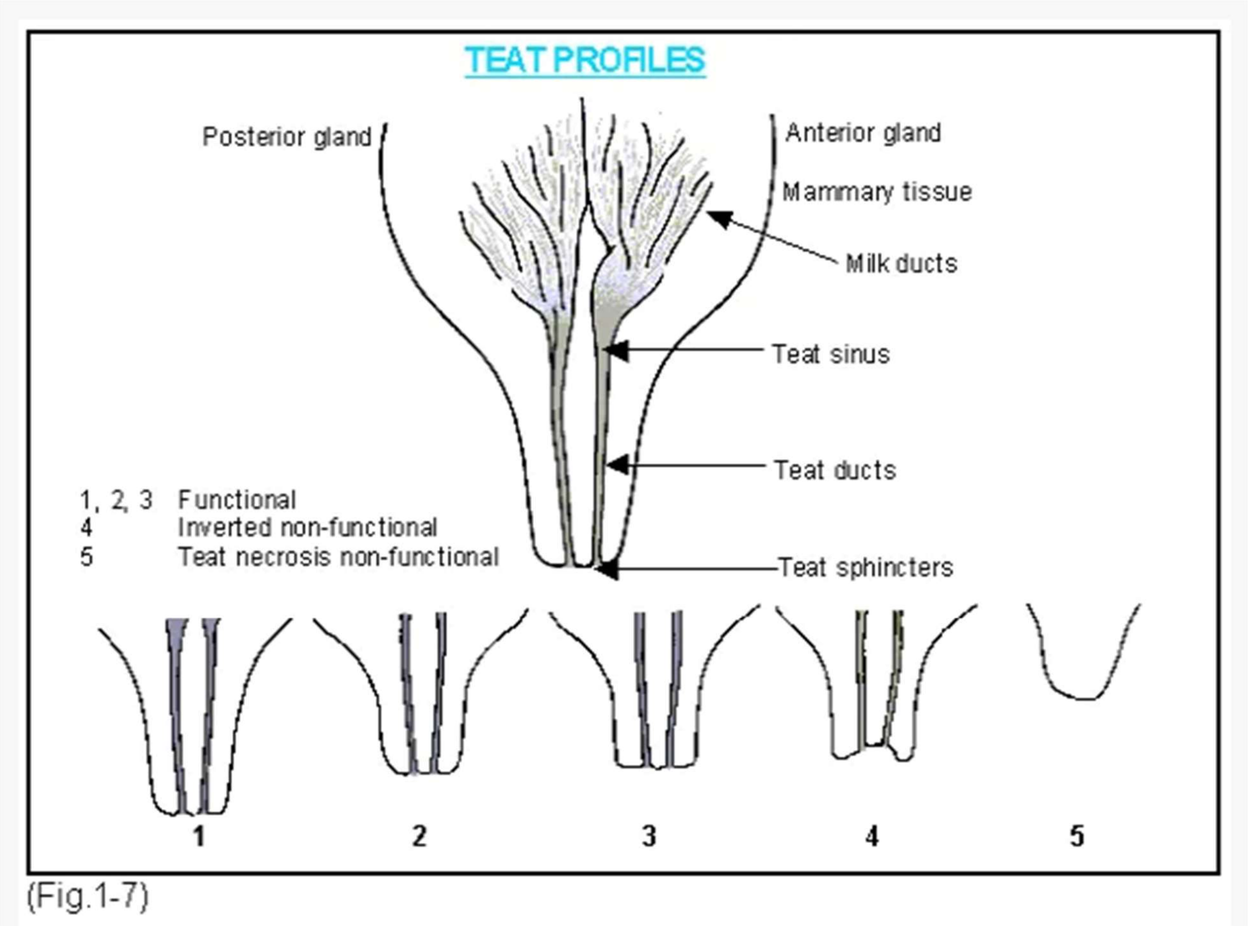

Figure 1. Image from Muirhead and Alexander (1997) illustrating the difference between functional and non-functional teats.

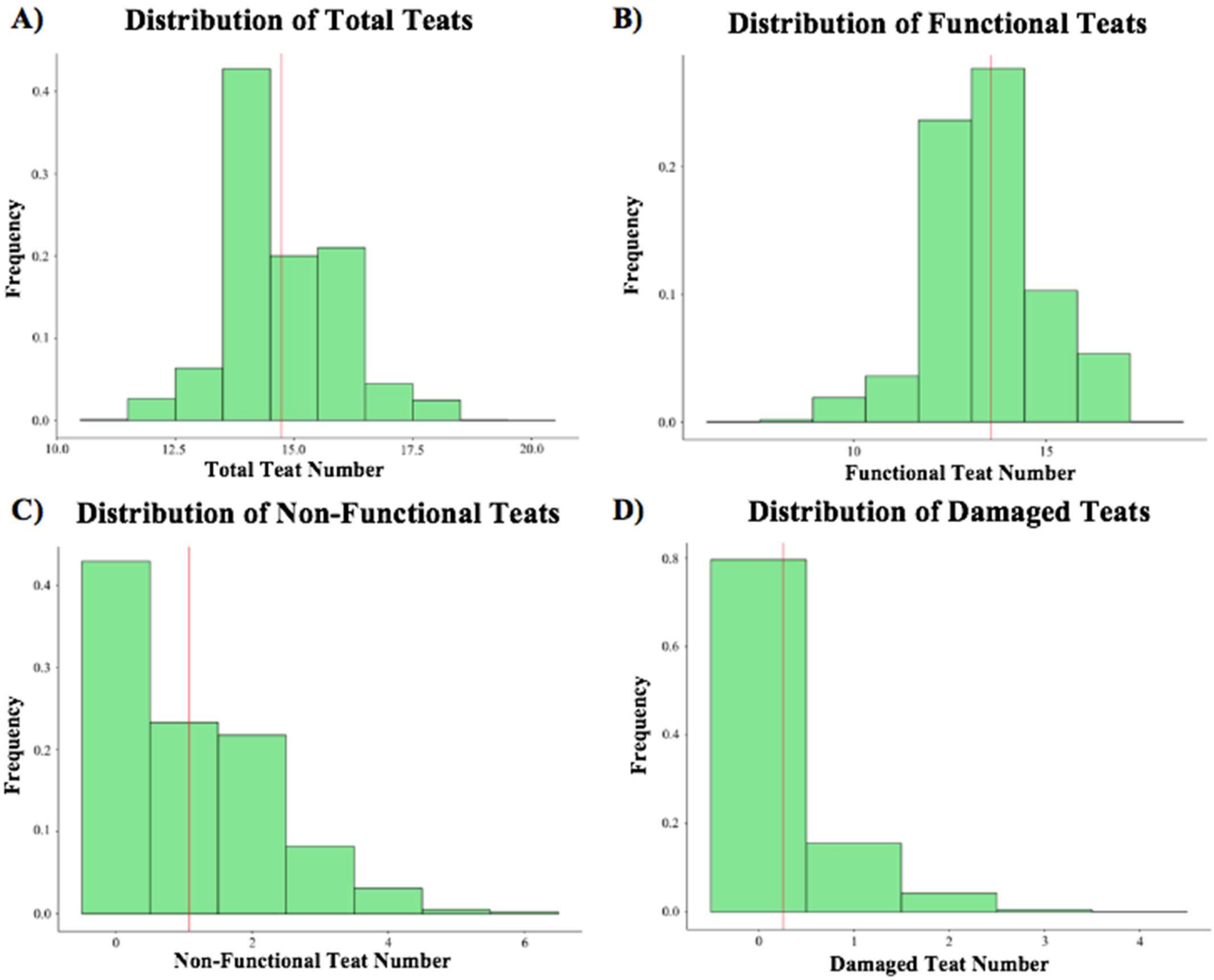

Figure 2. Histogram distributions of teat traits in the sample population with a red line indicating where the mean falls within the distribution. A) is total teat number distribution, B) is functional teat number distribution, C) is non-functional teat number distribution, and D) is damaged teat number distribution.

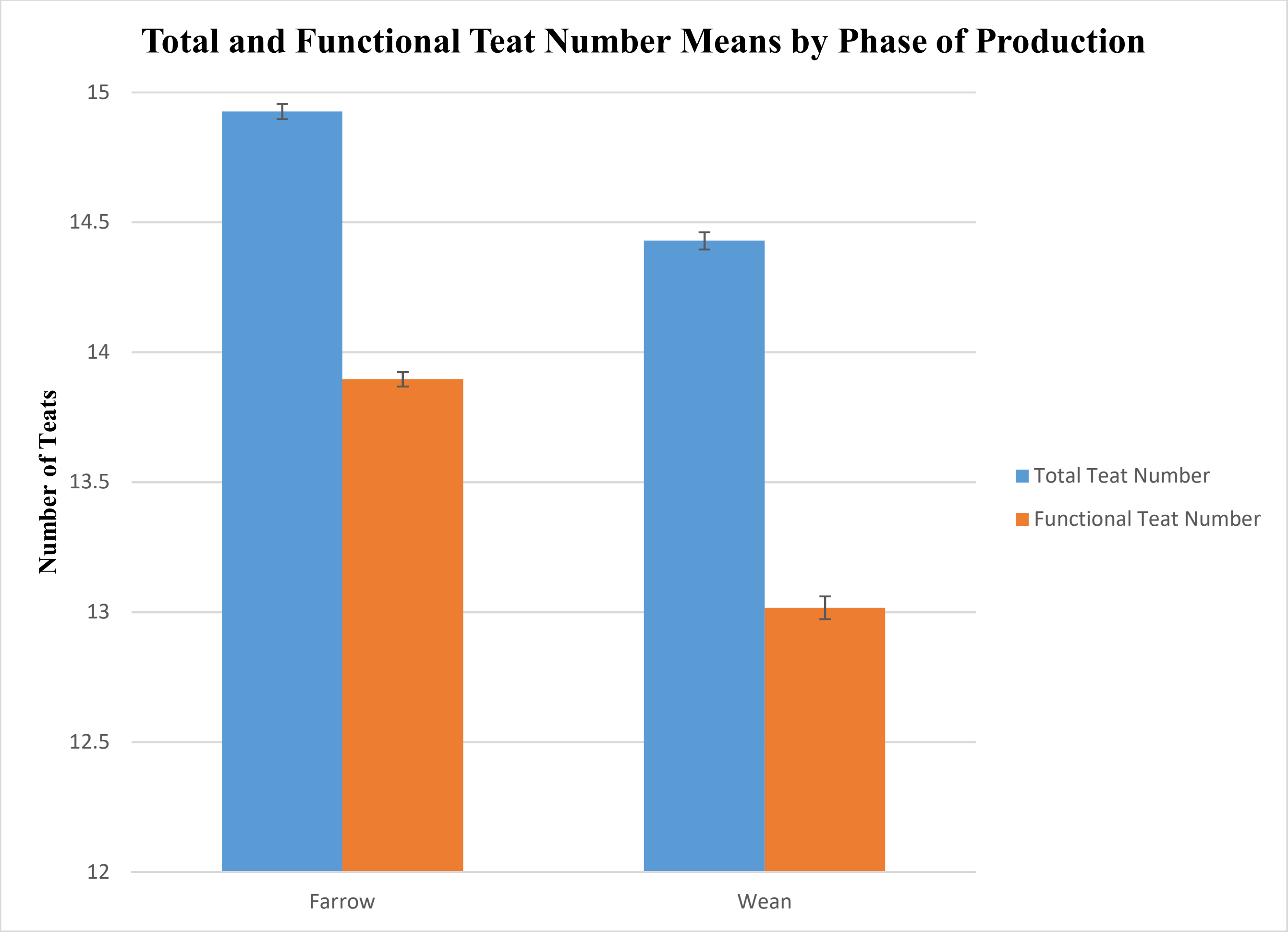

Figure 3. Comparison of total and functional teat number means by phase of production sampled. Table 1 contains the mean and standard error values.

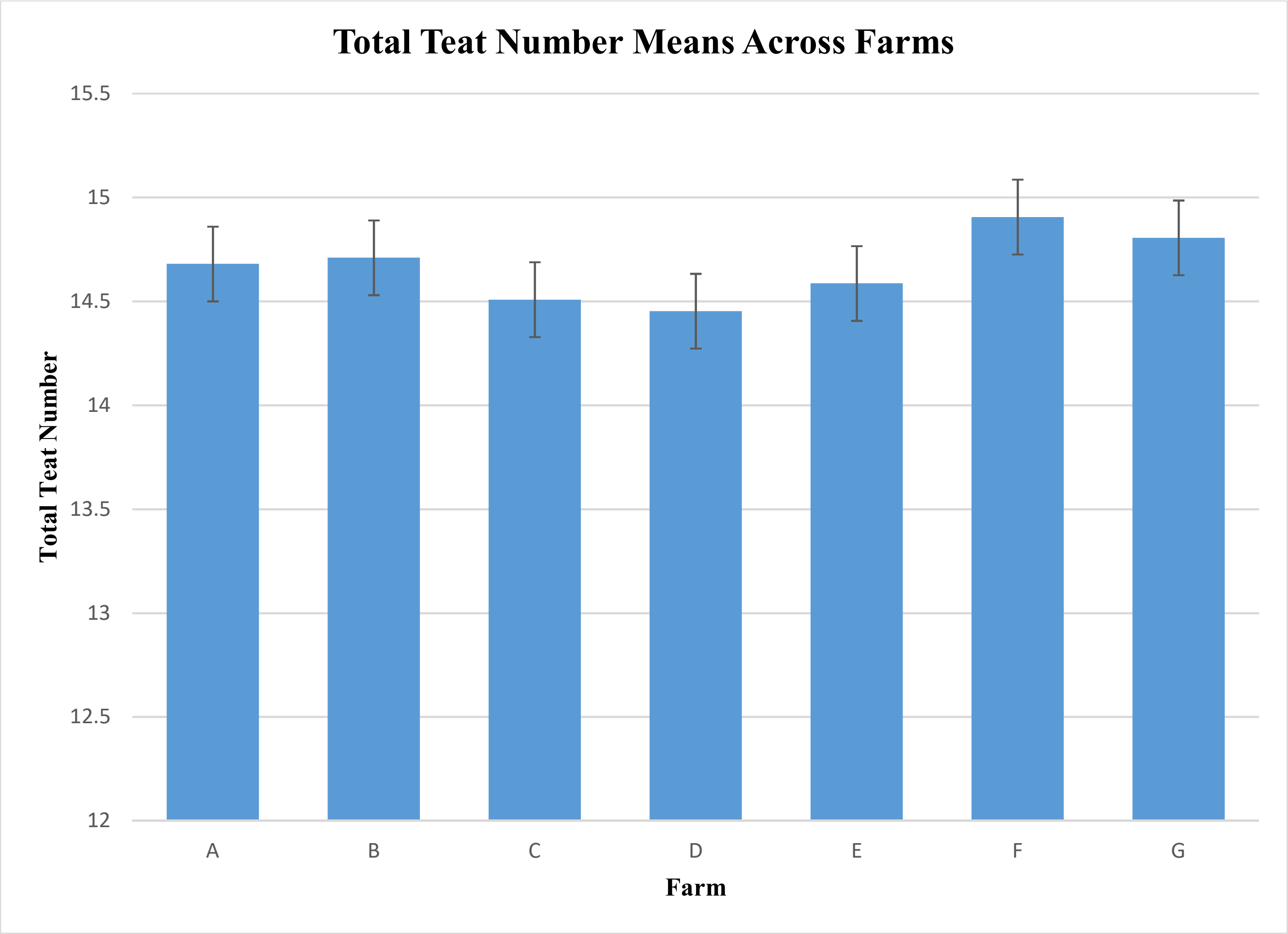

Figure 4. Comparison of the means for total teat number between farms. Table 2 contains the mean and standard error values.

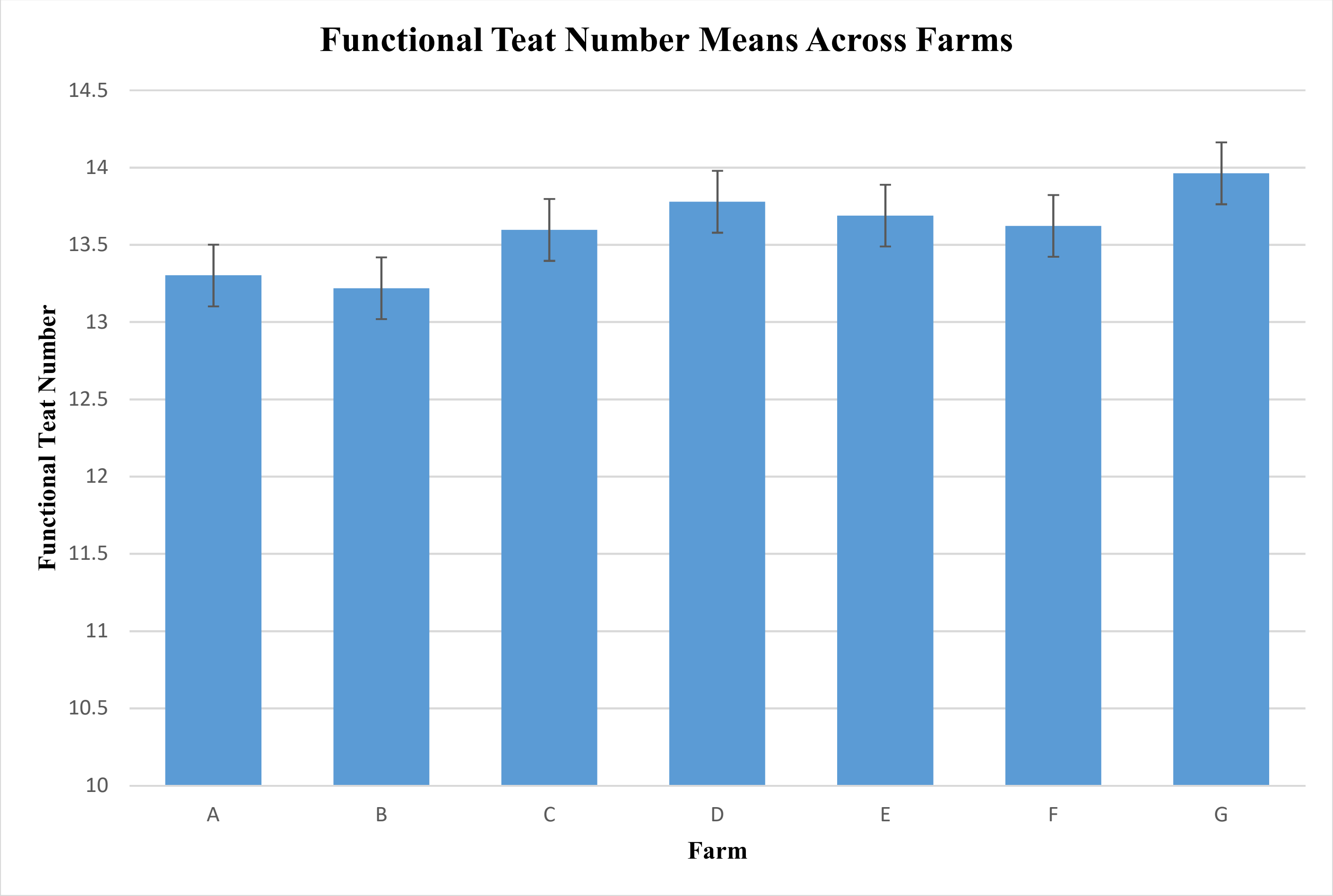

Figure 5. Comparison of the means for functional teat number between farms. Table 2 contains the mean and standard error values.

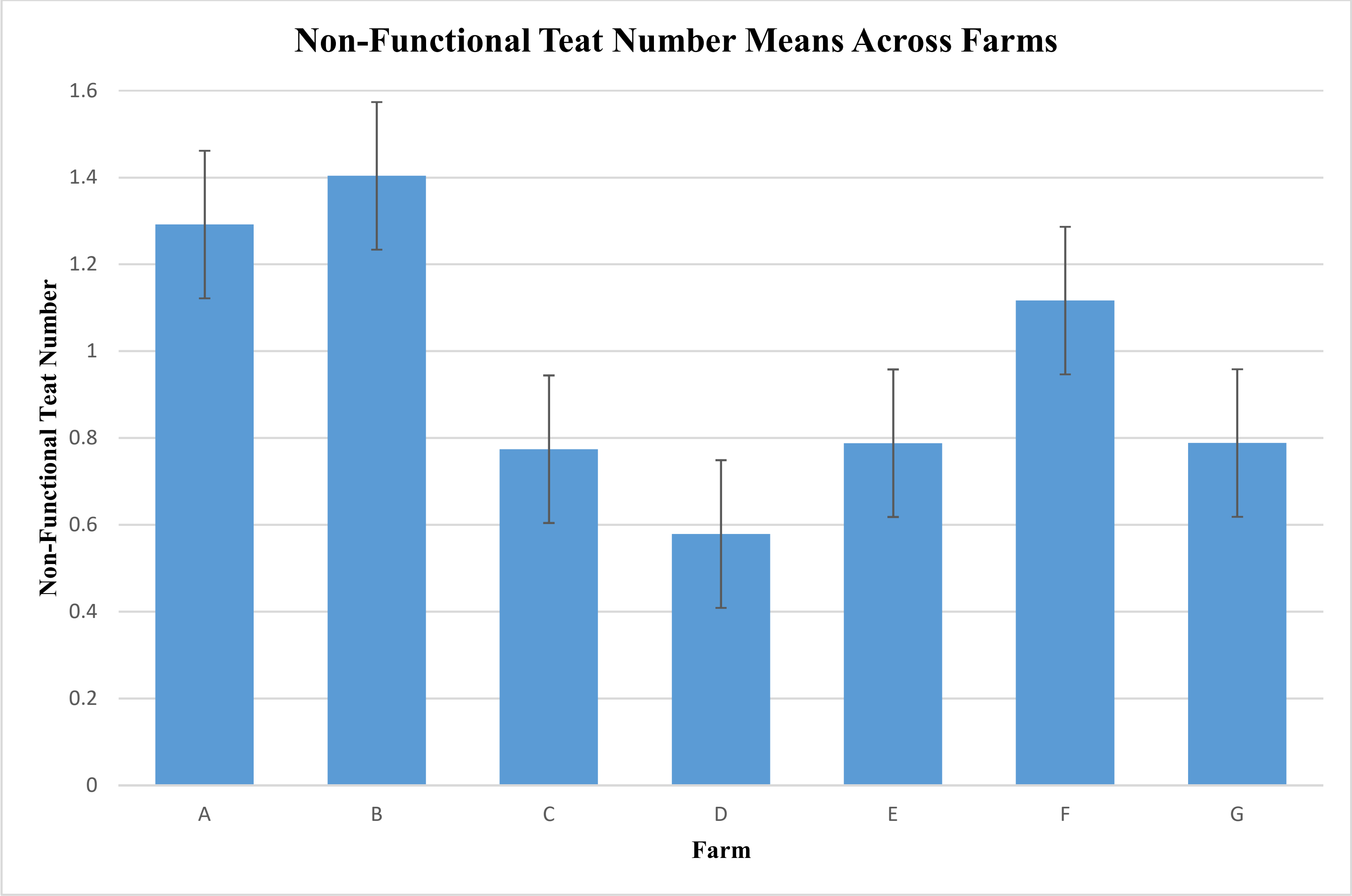

Figure 6. Comparison of the means for non-functional teat number between farms. Table 2 contains the mean and standard error values.

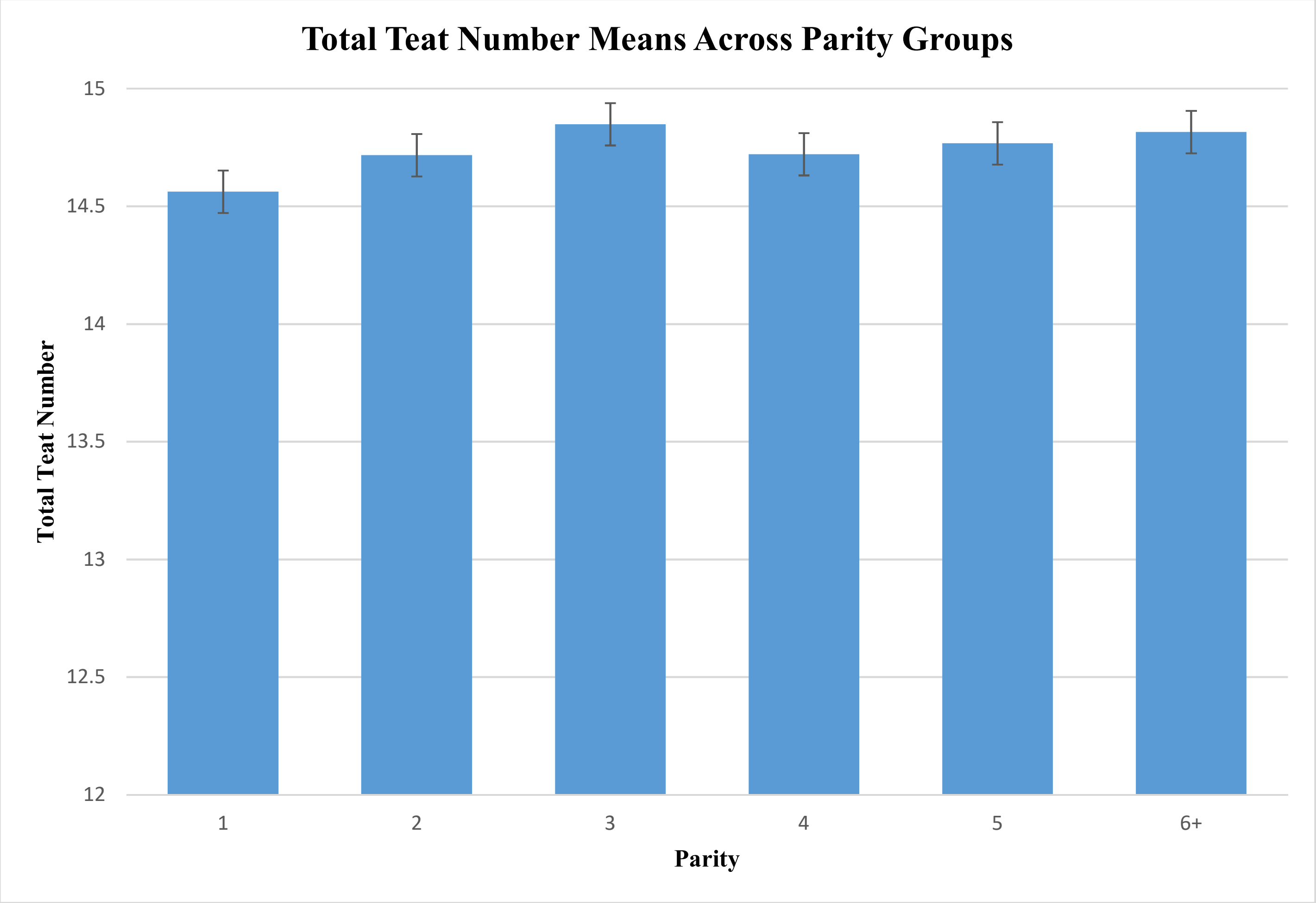

Figure 7. Comparison of the means for total teat number between parity groups. Table 2 contains the mean and standard error values.

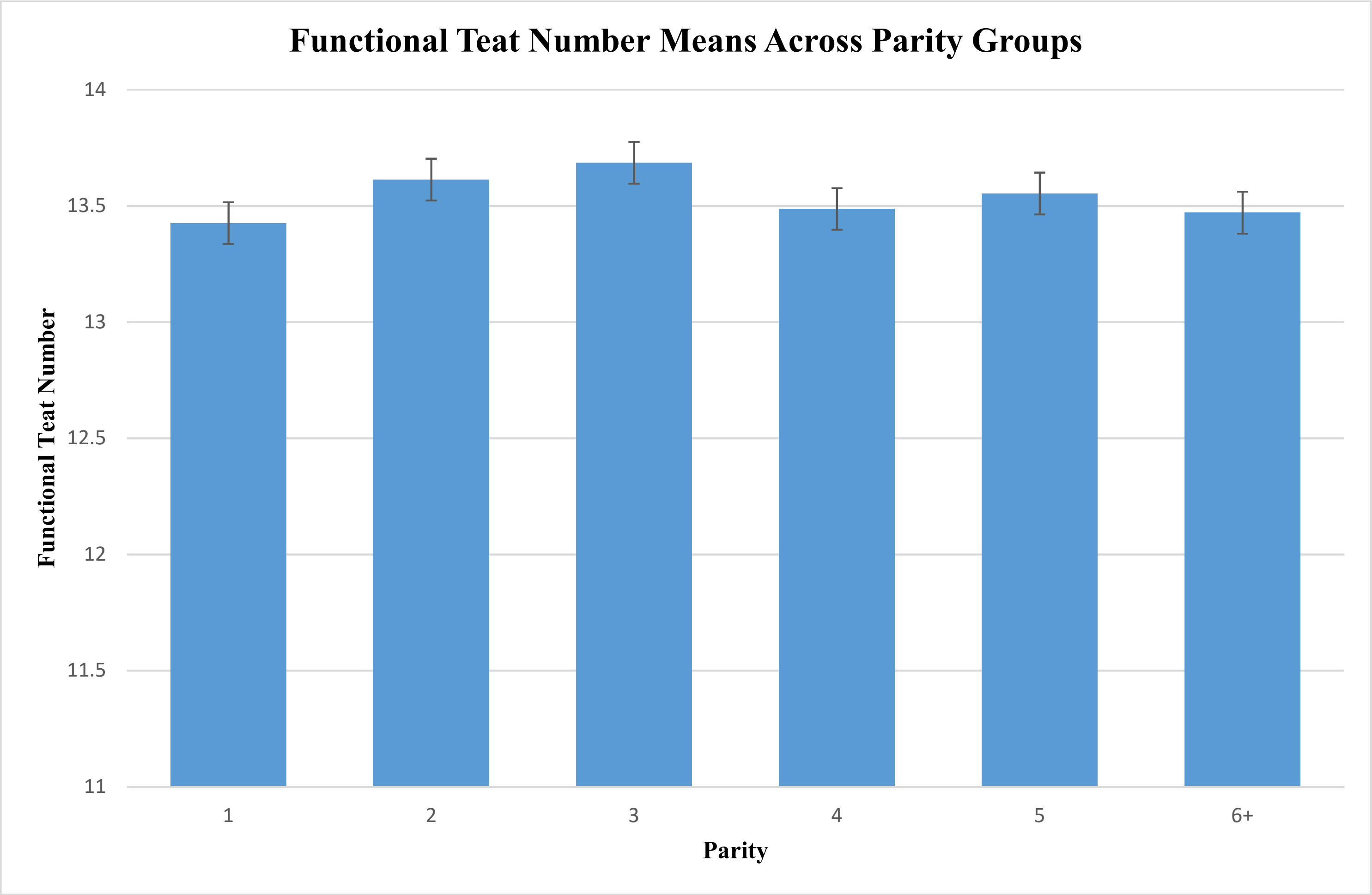

Figure 8. Comparison of the means for functional teat number between parity groups. Table 2 contains the mean and standard error values.

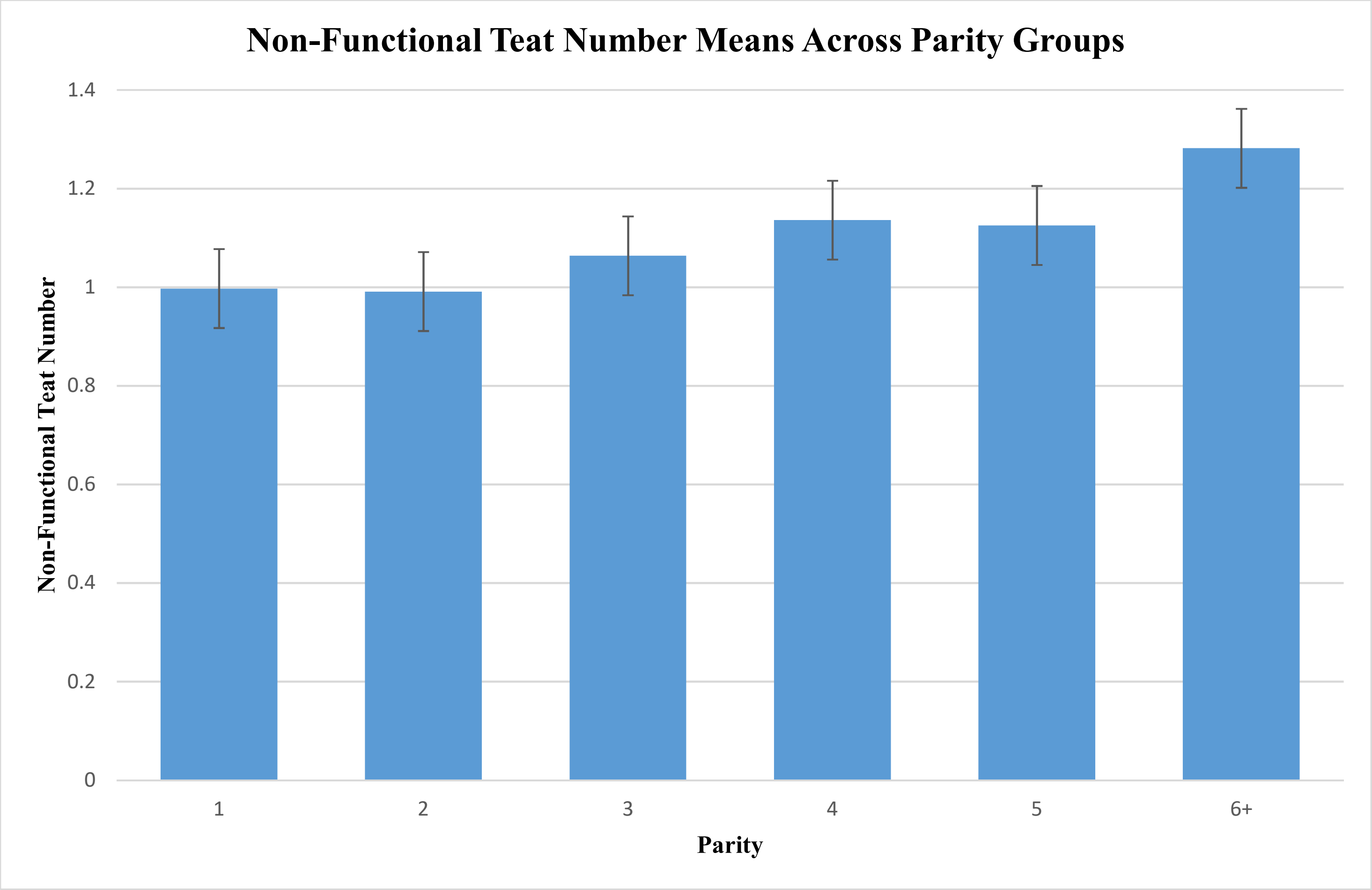

Figure 9. Comparison of the means for non-functional teat number between parity groups. Table 2 contains the mean and standard error values.