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Phenotypic Characterization of Rambouillet Sheep Expressing the *Callipyge* Gene: I. Inheritance of the Condition and Production Characteristics¹

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ABSTRACT: The objectives of this study were to determine the mode of inheritance of the *callipyge* gene and to evaluate the growth, ADFI, feed efficiency, reproductive performance, and wool growth of sheep that are heterozygous for the *callipyge* gene. Ewes (n = 236) with a normal muscle phenotype and genotype were mated to three heterozygous rams that expressed the *callipyge* gene. Lambs (n = 311) were subjectively classified at weaning (90 to 120d) according to muscle phenotype by a panel of three evaluators working independently. The *callipyge* muscle phenotype was expressed in 150 lambs, whereas 161 lambs expressed a normal muscle phenotype. The percentage of lambs expressing the *callipyge* muscle

phenotype (48.2%) did not differ ($P > .1$) from the expected 50%. Growth rate was similar for lambs of both phenotypes regardless of sex. Feed efficiency was superior ($P < .05$) for both male and female lambs with the *callipyge* muscle phenotype. Average daily feed intake was lower for male ($P < .02$) and female ($P < .004$) lambs with the *callipyge* muscle phenotype. Grease fleece weight and staple length at 12 mo were superior ($P < .03$) for ewes with a normal muscle phenotype. These results indicate that the *callipyge* gene in sheep is dominant when inherited from the paternal parent and lambs expressing the *callipyge* gene have increased feed efficiency and reduced ADFI.

Key Words: Sheep, Growth, Efficiency, Wool, *Callipyge*

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Introduction

Recently, a unique sheep phenotype has emerged in the U. S. commercial sheep population. Sheep with this phenotype are extremely muscular and are similar to double-muscled cattle in appearance. The name *callipyge* (from Greek *calli-*, beautiful; *-pyge*, buttocks) and the symbol CLPG have been proposed for this gene (Cockett et al., 1994). Little is known about the productivity of sheep with the *callipyge* gene. It has been suggested that sheep with the *callipyge* gene exhibit the negative characteristics (increased dystocia, delayed puberty, low milk production, etc.) shown by double-muscled cattle; however, no evidence in the scientific literature confirms this assumption.

Because of the sheep industry's need for a more heavily muscled market lamb and the lack of

knowledge about sheep with the *callipyge* gene, a series of studies was conducted to examine the production characteristics of sheep with this phenotype. The objectives of this study were to determine the mode of inheritance of the *callipyge* gene and to characterize wool production, growth rate, and feed conversion of sheep with this unique phenotype.

Materials and Methods

Breeding Animals. Normal-muscled ewes (n = 236) were mated to half-sibling 15/16 Rambouillet, 1/16 Dorset rams (n = 3) that were heterozygous for the *callipyge* gene. The rams themselves were produced by mating *callipyge* rams to normal females. Ewes were exposed to rams for a 54-d breeding season that began October 1. Ewes were maintained in one flock from the beginning of the breeding season until lambs were weaned. Ewes lambled unassisted in large pens (6 m × 12 m) in an open-air barn and lambs were weighed and ear-tagged for identification within 12 h of birth. Ewes remained in large pens for 10 d until ewes and lambs had bonded sufficiently. Ewes and lambs were moved to wheat pasture and remained there until lambs were weaned. Lambs had free access to creep

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feed (Table 1) from birth until weaning (90 to 120 d). Weaning weights were adjusted for age of lamb, age of dam, and type of birth and rearing.

Feeding Trial. Paternal half-sibling Rambouillet ram lambs ($n = 42$), ewe lambs ($n = 54$), and Hampshire \times Rambouillet crossbred wethers ($n = 24$) were assigned to a growing/finishing trial to evaluate feed efficiency and rate of gain differences between lambs of two muscle phenotypes. Lambs were approximately 4 mo of age at the initiation of the feeding trial. Lambs were sheared before the initiation of the feeding trial to facilitate phenotype classification and for improved performance while on gain test. Each lamb was classified subjectively according to muscle phenotype by a panel of three trained evaluators. Only lambs that were independently classified as *callipyge* by all three evaluators were used in the study. Paternal half-sibling ram lambs ($n = 21$) expressing the *callipyge* gene were divided randomly into three groups of seven. The remaining half-sibling ram lambs ($n = 21$) with a "normal" muscle phenotype also were divided randomly into three groups of seven lambs. Paternal half-sibling ewe lambs ($n = 27$) expressing the *callipyge* gene were randomly divided into three groups of nine lambs. Three groups of nine paternal half-siblings with "normal" muscling were randomly selected as controls. Twelve 4-mo-old crossbred (Hampshire \times Rambouillet) wethers expressing the *callipyge* gene also were compared to 12 paternal half-siblings with normal muscle phenotypes. Twelve crossbred wethers of each phenotype were randomly divided into two groups of six lambs.

Lambs were given ad libitum access in drylot to a 12% crude protein corn-soybean meal diet (Table 2). The diet exceeded NRC (1985) recommendations for growing/finishing lambs. Feed and orts were weighed daily for the calculation of feed intake and feed efficiency. Lambs were weighed every 7 d to monitor ADG, feed efficiency, and slaughter weight. Ram and

wether lambs were fed to an end point of 54.5 kg, and ewe lambs were fed to an end point of 50 kg. Ewe lambs were fed to a lighter final weight so that lambs of each sex were at a similar body composition at the end of the feeding period. Lambs were housed in an open-air barn equipped with fenceline feeders and automatic waterers. Animals were rotated weekly to a new pen to remove pen effects.

Wool. Ewe lambs were sheared on June 1 before the beginning of the gain test. All ewes were retained in the breeding flock and were sheared again on June 1 of their yearling year to determine 12-mo grease fleece weight and staple length.

Statistical Analysis. Data were analyzed using a chi-square goodness of fit test to determine whether the segregation of phenotypes was different from the 1:1 ratio for a single locus affecting muscle phenotype that would be expected if the sires were heterozygous. Growth rate, feed efficiency, and wool data were analyzed as a completely randomized design using the GLM procedures of SAS (1990). Least squares means for growth rate and feed efficiency were analyzed using a model that included sex, muscle phenotype, and their interaction. Least squares means were separated using a *t*-test.

Results

Of the 311 lambs weaned at 90 to 120 d of age, 150 (48.2%) expressed the *callipyge* muscle phenotype and 161 (51.8%) expressed a normal muscle phenotype. The percentage of lambs expressing the *callipyge* phenotype did not differ ($P > .1$) from the expected 50%. Within ram lambs, 67 (44%) expressed the *callipyge* muscle phenotype and 84 (56%) expressed a normal muscle phenotype. Within ewe lambs, 83

Table 1. Composition of creep diet

| Item | % (as-fed) |
|---|------------|
| Ingredient | |
| Cracked corn | 63.00 |
| Cottonseed meal | 10.00 |
| Soybean meal | 10.00 |
| Dehydrated alfalfa pellets | 7.50 |
| Cane molasses | 5.00 |
| Cottonseed hulls | 2.50 |
| Limestone | 1.00 |
| Salt | .50 |
| Ammonium chloride | .40 |
| Aureomycin 10 | .07 |
| Vitamin A, D, and E premix ^a | .03 |
| Chemical composition | |
| Crude protein | 16.00 |
| Calcium | .74 |
| Phosphorus | .37 |

^aVitamins (IU/kg of premix): A (130,820), D (13,100), E (375).

Table 2. Composition of finishing diet

| Item | % (as-fed) |
|---|------------|
| Ingredient | |
| Cracked corn | 67.50 |
| Cottonseed hulls | 10.00 |
| Cane molasses | 7.50 |
| Soybean meal | 5.00 |
| Dehydrated alfalfa pellets | 5.00 |
| Cottonseed meal | 2.70 |
| Limestone | 1.25 |
| Salt | .50 |
| Ammonium chloride | .50 |
| Aureomycin 10 | .04 |
| Vitamin A, D, and E Premix ^a | .01 |
| Chemical composition | |
| Crude protein | 12.20 |
| Calcium | .68 |
| Phosphorus | .30 |

^aVitamins (IU/kg of premix): A (130,820), D (13,100), E (375).

(51.8%) expressed the *callipyge* muscle phenotype and 77 (48.2%) expressed a normal muscle phenotype. The sex ratio of lambs expressing the *callipyge* gene did not differ ($P > .1$) from the expected 50%.

Least squares means for birth weights for ram and ewe lambs did not differ ($P = .4$) between phenotypes (data not shown). Ram lambs of both phenotypes were heavier ($P < .05$) at weaning than ewe lambs, but muscle phenotype did not ($P > .2$) influence weaning weight (Figure 1).

Feeding Trial. Average daily gain, ADFI, and feed efficiency for lambs of each phenotype are reported in Table 3. Average daily gain was not affected by muscle phenotype but was affected by sex. Ram lambs (.36 kg/d) gained faster than ewe lambs (.27 kg/d) regardless of phenotype.

Feed efficiency was affected by both muscle phenotype and sex. Rams, wethers, and ewes expressing the *callipyge* muscle phenotype gained more weight per unit of feed than half-siblings with a normal muscle phenotype. Rams were more efficient than ewes in their conversion of feed to gain. Feed intake was affected by muscle phenotype; rams, wethers and ewes expressing the *callipyge* gene consumed less feed than their normal-muscled half-siblings.

Wool. Ewes expressing the *callipyge* gene had lighter weight ($P < .01$) and shorter stapled ($P < .03$) fleeces than half-sibling control ewes (Table 4).

Discussion

Ewes experienced no difficulty in delivering lambs naturally. All lambs exhibited a normal muscle

phenotype at birth. At approximately 4 to 6 wk of age, the *callipyge* phenotype became apparent in the lambs. Lambs expressing the *callipyge* phenotype were approximately the same size at birth as half-siblings with a normal muscle phenotype. This is in conflict with the literature concerning birth weights of double-muscled calves. Double-muscled calves usually are 10 to 30% heavier at birth than normal calves and are also extremely heavily muscled at birth (Kieffer et al., 1971). The lack of dystocia experienced by ewes expressing the *callipyge* gene is in contrast to literature published on double-muscled cattle. Double-muscled cows are reported to have considerable calving problems (Kidwell et al., 1952; Kieffer et al., 1971; Hanset and Jar drain, 1979). In a review of literature published on double-muscled cows and calving ease by Menissier (1982), more than 85% of the double-muscled dams experienced extreme dystocia and 62% required caesarean sections to deliver calves. The size and shape of double-muscled calves in conjunction with the small pelvic size of the dams both contributed to the extreme dystocia problems observed in double-muscled cows (Menissier, 1982). Ewes that deliver lambs destined to express the *callipyge* muscle phenotype are not subjected to the pelvic-fetal incompatibilities that cows giving birth to double-muscled calves experience during parturition. When lambs expressing the *callipyge* gene are born, their muscle development is not different from that of normal-muscled lambs. The combination of normal birth weight and normal lamb shape allows lambs with the *callipyge* gene to be born with the same ease as normal muscled lambs. Growth performance of lambs

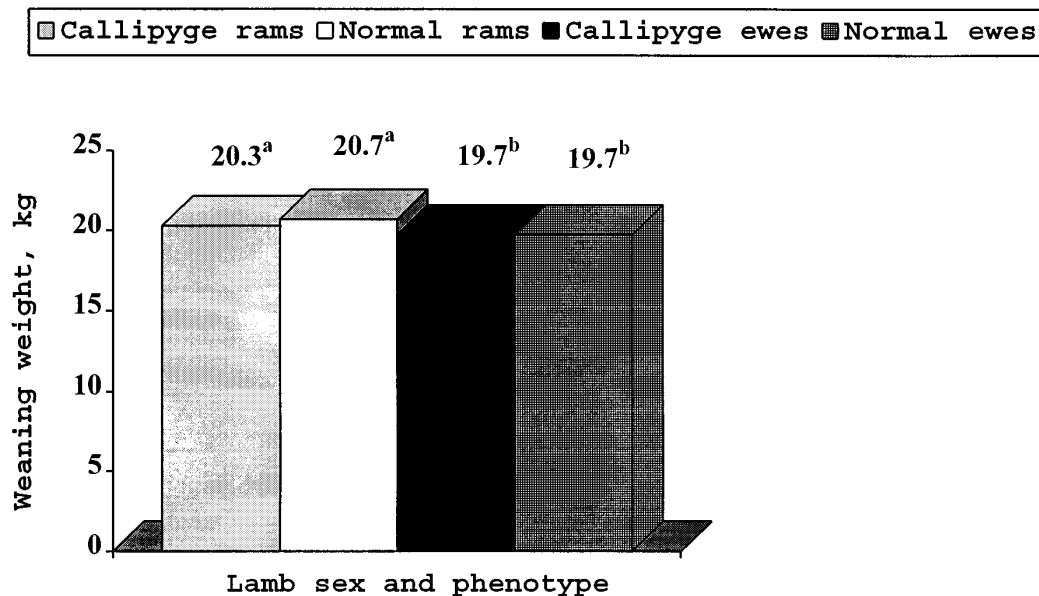


Figure 1. Least squares means for weaning weights for ram and ewe lambs expressing different muscle phenotypes. Means for each sex with different superscripts differ ($P < .05$). For ram lambs of each phenotype, $n = 21$. For ewe lambs of each phenotype, $n = 27$. Pooled SEM = .82.

Table 3. Least squares means for performance traits of ram, wether, and ewe lambs representing two muscle phenotypes

| Trait | Phenotype | | SEM | P-value |
|---------------------------------|------------------|--------|------|---------|
| | <i>Callipyge</i> | Normal | | |
| Average daily gain, kg/d | | | | |
| Rams, (n = 42) | .36 | .35 | .010 | .378 |
| Ewes, (n = 54) | .26 | .29 | .010 | .802 |
| Wethers, (n = 24) | .29 | .31 | .007 | .184 |
| Average daily feed intake, kg/d | | | | |
| Rams | 1.75 | 1.90 | .030 | .016 |
| Ewes | 1.48 | 1.68 | .030 | .004 |
| Wethers | 1.67 | 2.11 | .055 | .0002 |
| Feed conversion, gain/feed | | | | |
| Rams | .203 | .185 | .090 | .007 |
| Ewes | .173 | .165 | .090 | .050 |
| Wethers | .175 | .148 | .140 | .036 |

with the *callipyge* gene was not different from the performance of normal-musclled lambs during the preweaning period. This pattern of growth is similar to the growth pattern of double-musclled cattle during the preweaning period (Geay et al., 1982).

Lambs expressing the *callipyge* gene were easily distinguished from their paternal half-siblings with "normal" muscling. Lambs with the *callipyge* muscle phenotype were extremely muscular down their backs and were more expressively musclled in their hind legs. All lambs classified into the *callipyge* muscle phenotype had a distinct dorsal groove that extended caudally from the base of the neck to the dock. This intermuscular groove was located in the center of the back and was due to the large size of the longissimus muscle on each side of the spinous process of the vertebra. Another obviously enlarged muscle in lambs expressing the *callipyge* phenotype was the superficial gluteal ("jump" muscle), which is located on top of the rump. The superficial gluteal was very pronounced and contributed to the optical illusion that the lambs were "steep" in the rump. The last area that appeared to be enlarged in lambs with the *callipyge* gene was the twist. This area, located just ventral to the rectum, is dominated by the gracilis and adductor muscles. Lambs with the *callipyge* gene were much deeper in the twist and appeared to have more expression of muscle on the inner portion of the rear leg. Surpris-

ingly, the expression of *callipyge* muscle phenotype was not apparent in the newborn lamb. Rather, the condition became noticeable at about 4 to 6 wk of age in lambs that were receiving adequate nutrition. Triplet, twin, and orphan lambs on a lower plane of nutrition expressed the *callipyge* phenotype 4 to 6 wk later when they began to "catch up" to single-born lambs in terms of nutrient intake and physiological maturity.

The genetic hypothesis of this experiment was that the inheritance of the *callipyge* gene was due to a single, dominant gene. According to Mendelian genetic theory, the normal segregation of dominant phenotypes when one parent is a heterozygote and the other parent is a non-carrier is 1:1. These data suggest that the *callipyge* muscle phenotype is controlled by a single, dominant gene when the gene is inherited as the paternal allele. Additionally, there was equal segregation of the *callipyge* phenotype across both sexes. In cattle, the mode of inheritance of the double-musclled condition is not consistent between biological types of cattle. In British breeds of cattle, the expression of the double-musclled condition is due to a partially recessive gene (Kidwell et al., 1952). In the Piedmontese breed, the condition is caused by a partially dominant to completely dominant gene (Ramondi, 1964). However, the same gene locus is responsible for the double-musclled condition in both

Table 4. Least squares means for 12-month fleece weight and 12-month staple length for yearling Rambouillet ewes expressing different muscle phenotypes^a

| Item | Phenotype | | SEM | P-value |
|-------------------|------------------|--------|-----|---------|
| | <i>Callipyge</i> | Normal | | |
| Fleece weight, kg | 5.5 | 6.2 | .18 | .01 |
| Staple length, cm | 8.5 | 9.2 | .19 | .03 |

^an = 27 ewes of each phenotype.

British and European breeds of cattle (Rollins et al., 1972). In swine, the halothane gene is a recessive gene with incomplete penetrance (Smith and Bampton, 1977; Reik et al., 1983). The negative reaction to halothane gas is influenced by modifier genes (Reik et al., 1983).

Feeding Trial. Lambs with the *callipyge* gene had similar average daily gains as their half-siblings with a normal muscle phenotype. In contrast, several reports have indicated that steers and bulls with double muscling had lower average daily gains than normal-muscled controls (Nott and Rollins, 1973; Geay et al., 1982; Arthur et al., 1990). In a study comparing double-muscled Pietrain pigs with normal-muscled French Landrace pigs, Landrace pigs had higher average daily gains than Pietrains (Henry and Sellier, 1982).

Lambs with the *callipyge* gene were superior in feed efficiency when compared to control half-siblings. Similarly, several researchers (Ramondi, 1964; Nott and Rollins, 1973; Geay et al., 1982) have reported that double-muscled cattle gain more efficiently than normal cattle. However, others (Arthur et al., 1990) have reported that double-muscled cattle require more feed per unit of gain than normal cattle. Henry and Sellier (1982) reported that feed conversion was similar between normal and double-muscled swine breeds.

Lambs expressing the *callipyge* muscle phenotype consumed less feed per day than control half-sibling lambs. Feed intake and appetite of homozygous double-muscled cattle has been reported to be lower than that of both heterozygous double-muscled and normal-muscled cattle (Holmes and Ashmore, 1972; Thiessen and Rollins, 1982). It has also been reported that double-muscled cattle have a lower intake capacity than normal-muscled cattle of the same breed (Geay et al., 1982). Similar results have been published by Henry and Sellier (1982) in studies with normal- and double-muscled swine breeds.

Wool. Grease fleece weight and staple length were affected by muscle phenotype. Fleece weights of ewes with the *callipyge* gene were 12.7% lower than fleece weights of half-siblings. Staple length was 8.7% shorter for ewes with the *callipyge* gene than for controls. The reduction in fleece weight and staple length for ewes with the *callipyge* gene is likely due to the increased utilization of amino acids for muscle growth rather than wool growth. Even though wool production was negatively affected by the *callipyge* gene, the wool production of the ewes in this study was still very acceptable by industry standards.

Implications

The *callipyge* muscle phenotype has been observed in the United States commercial sheep population for approximately 10 yr. Many questions remain concerning the commercial potential of sheep with the *callipyge* gene. Callipyge lambs in this study were

similar in average daily gain, consumed less feed, and had superior gain:feed ratios compared to normal-muscled, half-sibling controls. The results from this study indicate that lambs with the *callipyge* gene may help increase the efficiency of lamb production through improvement in feed conversion.

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