Plenty of Lamb, But Tough to Eat: Understanding the Callipyge Phenomenon

Nancy Jean Kerr
Graduate Research Assistant
Division of Animal and Veterinary Science
West Virginia Agricultural and Forestry Experiment Station

Keywords: Lamb, Callipyge, Muscular Hypertrophy, Genetic Anomalies

TABLE OF CONTENTS

ABSTRACT……………………………………………………………….…….3

INTRODUCTION…………………………………………………………………4

CHARACTERISTICS……………………………………………………...5

INHERITANCE……………..…………………………………………………..8

ECONOMIC FACTORS……………………………….……………….....12

PROCESSING FOR TENDERNESS……………………………………………..13

SUMMARY AND CONCLUSIONS..………………………………………………15

REFERENCES…………………………………………………………………….16

GLOSSARY OF TERMS…………………………………………………………18

Plenty of Lamb, But Tough to Eat: Understanding the Callipyge Phenomenon

Abstract

In 1983, a ram lamb exhibiting obvious muscular hypertrophy in the hindquarters was born into a commercial Dorset flock in Oklahoma. The ram produced offspring expressing the same phenotype, which is referred to as callipyge (Greek: *calli*- beautiful + -*pyge* buttocks). Lambs expressing the gene have superior feed efficiencies and decreased feed intakes. They produce leaner, higher yielding carcasses, but have decreased tenderness of the loin. Calpastatin activity is elevated in loin eye muscle of callipyge lambs compared to normal lambs at slaughter and during postharvest aging. Only heterozygous offspring inheriting the mutation from the sire express the callipyge phenotype. This unique mode of inheritance is referred to as "polar overdominance". A 1:1 sex-independent segregation ratio of callipyge and normal offspring resulted from mating callipyge rams and normal ewes, indicating an autosomal dominant model. However, matings between callipyge ewes and normal rams did not fit the autosomal dominant model. Offspring that inherited the callipyge mutation from their dam did not express the phenotype; whereas, offspring that inherited the same mutation from their sire expressed the phenotype. Thus, a parent-of-origin effect was observed, leading researchers to suggest a possible role of genetic imprinting. In callipyge lambs killed at 8 weeks of age, reduced protein degradation rather than increased protein synthesis seems to be responsible for enhanced growth of specific muscles. Total production costs are lower in callipyge lambs due to a decrease in postweaning feed costs and an improved feed efficiency. With proper post-harvest handling of the meat, callipyge lamb has the potential to decrease the cost of lamb to consumers and increase profitability of the lamb industry.

Plenty of Lamb, But Tough to Eat: Understanding the Callipyge Phenomenon

Introduction

Lamb production in the United States has been declining since 1942. Many factors have contributed to the decline in the number of sheep in production and lambs being produced. These factors include losses due to predation, natural disasters, decreased availability of grazing lands, loss of government incentive support programs, decreased consumer demand, the whole-flock scrapie eradication program, ewe and lamb mortality due to diseases, disorders occurring at parturition such as Ringwomb, and decreased fecundity, resulting from both early and late embryonic mortality. The rate of decline in the number of sheep in production has been dramatic compared to the rate of decline in total production of meat from lamb. Genetic selection for increased lamb carcass weight, increased size at maturity, and the use of large breed terminal sires has reduced the rate of decline in total production of lamb.

Consumers of lamb in the United States, with the exception of some traditional ethnic consumers, prefer large loin chops that are low in fat and cholesterol (Shelley et al, 1970; Busboom et al., 1998). In 1983, a ram lamb exhibiting pronounced muscular hypertrophy particularly in the hindquarters, was born into the Moffat commercial Dorset flock near Piedmondt, Oklahoma. The ram subsequently produced some offspring expressing the same phenotype. Lambs exhibiting the phenotype have increased muscling of the loin and a leaner carcass than normal lambs in addition to the enhanced muscling of the hindquarters. Noelle Cockett and colleagues at Utah State University identified the mutant gene responsible for the trait. The trait is referred to as callipyge (Greek: *calli-* beautiful + *-pyge* buttocks) and the symbol CLPG represents this gene (Cockett et al., 1994).

Many sheep producers in the United States have not been interested in production of callipyge lambs. They associate callipyge with double-muscling in cattle, which often leads to reduced female fertility, increased susceptibility to respiratory illness, and an increased incidence of difficult births. Despite the negative characteristics of double-muscling in cattle and sheep, producers in Europe select for that phenotype (Leroy, 2000). Not only are double muscling and callipyge different traits, the genes for the two traits are located on different chromosomes (double-muscling on chromosome 2; callipyge on chromosome 18). The main difference between the callipyge phenotype and the double-muscling phenotype is that double muscling results from hyperplastic growth and callipyge from hypertrophic growth. Hyperplasia occurs prenatally (in late gestation) as a result of an increase in the number of mitotic cell cycles, yielding more muscle fibers. Hypertrophy occurs postnatally as a result of an increase in size of muscle fibers, which is accomplished by the accumulation of cells and/or cell products over time.

In this circular, the known facts about callipyge lamb are reviewed and the possibilities for its contribution to the American sheep industry are evaluated. Possible approaches to managing the introduction of the gene through terminal sires and to post-harvest processing of the product are presented.

CHARACTERISTICS

Lambs expressing the callipyge gene have superior feed efficiencies, higher dressing percentages, larger longissimus (loin eye) muscle areas, and higher cutabilities than normal-muscled half-siblings (Jackson et al., 1997). Muscles exhibiting hypertrophy in callipyge lambs have higher percentages of fast-twitch glycolytic muscle fibers and lower percentages of slow-twitch oxidative muscle fibers (Koohmaraie et al., 1995; Carpenter et al., 1996; Jackson et al., 1997). However, the hypertrophy develops only after three weeks of age (Koohmaraie et al., 1995), and may not be noticeable until the lamb has reached a bodyweight of 40 to 50 lbs. Thus, from a production perspective, callipyge lambs do not pose an increased risk of difficult birth for the dam. In fact, Jackson et al. (1997) found that lambs that express the callipyge gene are comparable to normal-muscled half-siblings in birth weight, weaning weight, and growth rate. Feed efficiency is improved and feed intake is decreased in callipyge lambs compared to normal lambs (Jackson et al., 1997).

The callipyge gene has negative influences on wool traits. Decreases of 13% in fleece weight and 9% in staple length in callipgye ewes, compared with normal ewes, were reported by Jackson et al. (1997). However, wool produced by a callipyge animal is acceptable by industry standards.

Lambs expressing the callipyge gene can be distinguished easily from lambs with normal muscling. According to Jackson et al. (1997), three major areas can be observed to identify lambs exhibiting the callipyge phenotype. Besides the pronounced heavy muscling in the hindquarters, lambs with the callipyge phenotype display a distinct intermuscular groove that extends from the neck down to the dock. The groove, in part, is due to the enlarged loin eye muscle on each side of the spinous projections of the vertebra. Secondly, the superficial gluteal muscle, part of the sirloin located on top of the rump, is very pronounced and contributes to the appearance of a 'steep' rump. The final area of enlargement, the twist, located ventral to the rectum, and facilitated by the gracilis and adductor muscles, contributes to the enhanced appearance of the inner portion of the hind leg (Jackson et al., 1997).

Not all of the muscles are affected in lambs expressing the callipyge phenotype, and not all muscles are affected equally. Muscles influenced the most, that can be perceived visually in live lambs, are those located in the pelvic and torso regions. The sirloin (gluteus group) and inside leg (semimembranosus and adductor) muscles experience significant increases in weight. In one study, the inside leg muscle from callipyge lamb carcasses expressed the greatest percentage increase in weight: a 38% increase (Koohmaraie et al., 1995). The thoracic muscles tend to be affected less by the callipyge gene. The thoracic muscles increase up to 20% in size over those of normal lambs whereas, the pelvic and torso muscles experience increases up to 42% and 50% over normal lambs, respectively. The shoulder (infraspinatus and supraspinatus) muscles are not affected in callipyge lambs.

In collaboration with the USDA-ARS in Clay Center, Nebraska, Lorenzen et al. (2000) at Texas A & M University studied the effects of the callipyge genotype on protein turnover in muscles. Callipyge lambs killed at 5, 8, and 11 weeks of age had greater total protein and protein:DNA ratio (an indicator of cell size) than normal lambs in loin eye and biceps femoris (bottom round muscle), but not in the shoulder muscles and diaphragm. In the lambs killed at 8 weeks, synthesis, degradation and net accretion of protein were studied. Fractional rates of both synthesis and degradation of protein were lower in loin eye and bottom round muscle of callipyge than of normal lambs, yet these muscles were heavier in the callipyge lambs. The researchers suggested that the muscling advantage in callipyge was "… maintained through a reduction in the rate of protein degradation rather than an increase in the rate of protein synthesis." In contrast, protein accretion in the liver was lower in the callipyge than in the normal lambs; both synthesis and degradation of protein were increased, but the increase in rate of degradation was greater than the increase in rate of synthesis.

Callipyge animals tend to be more desirable than normal animals for several carcass and meat characteristics (Koohmaraie et al., 1995; Jackson et al., 1997). In callipyge lamb carcasses, ribeye area is increased by 30% to 50%, and fatness (subcutaneous, intermuscular, intramuscular, and perinephric) is decreased by about 50% compared to normal lamb (Duckett, 2000).

In terms of retail yield of the callipyge carcass, the shoulder is similar to the yield of normal carcasses (Jackson et al., 1997). The reason for this is that the muscles of the shoulder (infraspinatus and supraspinatus) are not enlarged. This is advantageous because the least valuable retail cut from a lamb carcass is the shoulder. Therefore, it is beneficial for the shoulder to represent a smaller percentage of the carcass weight. The largest difference in retail yield is in the leg. The leg is the largest retail cut from a lamb carcass and has the highest retail value. Because the inside leg muscle is enhanced the most, the callipyge gene has the ability to be economically advantageous over normal lamb. Therefore, one would think that a genetic mutation with a unique inheritance pattern that enhances muscles of high economic value and decreases postweaning production costs is too good to be true.

Unfortunately, the major problem with the callipyge condition is its negative effect on meat tenderness. Loin chops from callipyge carcasses are 32 to 102% tougher than those from normal lamb (Duckett, 2000). The loin eye is the major muscle marketed in lamb. In callipyge lamb, the loin eye is less tender than the corresponding muscle from normal carcasses (Koohmaraie et al., 1995). Calpastatin activity, correlated with toughness, was greater in the loin eye of callipyge than normal lambs by 5 weeks of age (Lorenzen et al., 2000). Koohmaraie et al. (1995) observed that calpastatin activity in the callipyge loin eye was 82.8% greater than in the loin eye from normal lambs at the time of slaughter. The difference was even more pronounced at 7 and 21 days postmortem, because activity decreased with aging in the normal muscle but not in the callipyge muscle. Koohmaraie et al. (1998) proposed that the high calpastatin activity inhibits proteolysis and postmortem aging, resulting in increased toughness. Warner-Bratzler shear force, a measure of toughness, was greater for the callipyge loin eye, measured at 1, 7, and 12 days postmortem, by 45, 112, and 145%, respectively, compared to the normal muscle (Koohmaraie et al., 1995). Increased toughness seemed to be limited to the callipyge loin and shoulder, with little or no effect on the leg.

INHERITANCE

Cockett et al. (1994) observed a 1:1 sex-independent segregation of the callipyge phenotype in 412 lambs, with 203 (49.2%) callipyge and 209 (50.8%) normal lambs produced from the controlled matings between male descendants of the founder ram displaying the callipyge phenotype and unrelated, normal females. One hundred, thirty-three lambs, of both pedigrees, were genotyped. Further matings were performed between either normal rams (*clpg/clpg*, unrelated to the founder sire) or callipyge male descendents of the founder sire (*CLPG/clpg*) and callipyge ewe descendents of the same founder sire (*CLPG/clpg*).

The 1:1 segregation ratio of callipyge and normal offspring that resulted from the mating of callipyge rams and normal ewes led the researchers to suggest an autosomal dominant model (Cockett et al., 1996). However, matings between callipyge ewes (*CLPG/clpg*) and normal rams (*clpg/clpg*), referred to as a reciprocal cross, did not yield callipyge offspring and this did not fit the autosomal dominant model. Reciprocal-cross offspring were then genotyped, and a clear pattern of segregation was displayed (Cockett et al., 1996). Only normal phenotyped offspring were produced from the clpg/clpg (sire) x CLPG/clpg (dam) matings. Offspring having inherited the CLPG mutation from their dam (clpg*pat* x CLPG*mat*) did not express the phenotype. In contrast, offspring that inherited the same mutation from their sire expressed the phenotype, which pointed toward a parent-of-origin effect.

Under an autosomal dominant model, the mating of two heterozygous parents would be expected to produce 75% callipyge and 25% normal offspring. However, Cockett et al. (1996) reported that the mating resulted in 22% callipyge and 78% normal offspring. Genotyping of the offspring revealed that the inactive CLPG*mat* allele suppressed the active CLPG*pat* allele. The resulting pattern of segregation, in which only heterozygous offspring that inherited the mutation from their sire express the callipyge phenotype, is known as polar overdominance (Figure 1; Cockett et al., 1996).

Figure 1. Characteristic pattern of polar overdominance. The phenotypes (and genotypes in parentheses) obtained by mating heterozygous callipyge rams with callipyge ewes approximate 75% normal phenotype (25% CLPG/CLPG, 25% clpg/CLPG, and 25% clpg/clpg) and 25% callipyge phenotype (CLPG/clpg).

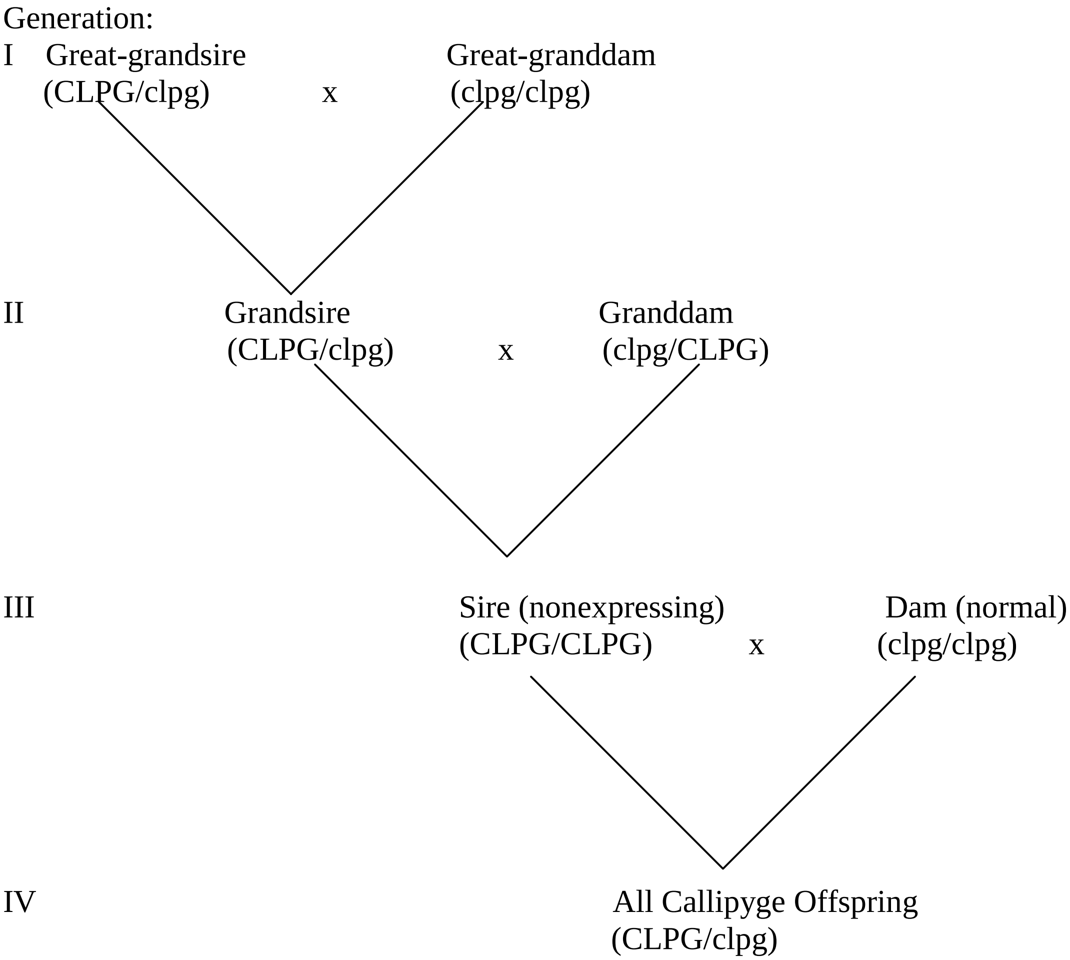
CLPG*pat*/clpg*mat* ram X CLPG*pat/*clpg*mat* ewe:

	CLPG	clpg
CLPG	CLPG*pat*/CLPG*mat* normal	clpg*pat*/CLPG*mat* normal
clpg	CLPG*pat*/clpg*mat* callipyge	clpg*pat*/clpg*mat* normal

Matings between non-expressing CLPG/CLPG rams and normal clpg/clpg ewes are expected to yield 100% callipyge offspring (Figure 2; Generations III and IV). That is, the maternal allele should be reactivated once it is passed through the paternal germline. However, this reactivation is not absolute. Cockett et al. (1996) reported that mating non-expressing CLPG/CLPG rams and normal clpg/clpg ewes yielded 91% (30/33) callipyge offspring. In a second study (Cockett et al., 1999), mating non-expressing CLPG/CLPG rams with normal clpg/clpg ewes produced 98% (111/113) callipyge offspring.

Cockett et al. (1996) suggested that conventional selection programs could not deal appropriately with genes exhibiting polar overdominance. Maintaining a flock of non-expressing carriers of the callipyge allele would be difficult and costly for the producer to have all replacement animals genotyped. One could suggest the maintenance of a small flock of identified CLPG/CLPG rams (Figure 2, Generation III) and collection and storage of semen for use in a terminal crossing program in flocks of normal clpg/clpg ewes to produce over 90% phenotypically callipyge offspring for slaughter.

Figure 2. Pedigree describing the breeding program necessary to yield nearly all callipyge offspring in the fourth generation. The mating in Generation I will yield 50% CLPG/clpg : 50% clpg/clpg. Male offspring with a CLPG/clpg genotype mated to clpg/CLPG females, in Generation II will yield 25% CLPG/CLPG; 25% clpg/clpg; 25% CLPG/clpg; 25% clpg/CLPG. Mating a non-expressing homozygous callipyge ram to normal ewes (Generation III) will yield callipyge offspring (Generation IV), assuming reactivation of the maternal allele passed through the male germ line.



The parent-of-origin effect observed for segregation of the callipyge phenotype led Cockett et al. (1996) to suggest a possible role of parental imprinting, but callipyge differs from conventional imprinting in that homozygous individuals do not express the phenotype. The regions homologous to the distal part of the ovine chromosome 18 correspond to the distal part of mouse chromosome 12 and the distal part of human chromosome 14, both of which are known to harbor imprinted regions (Cockett et al., 1996).

Cockett et al. (1996) devised two models to account for the observed segregation pattern. In the first model, the callipyge phenotype occurs only when a gene product is absent, such as a regulator of muscle growth. The normal form of the gene is maternally imprinted, therefore the maternal allele is not expressed while the paternal normal allele is active. The only genotype without expression of the normal form of the gene is CLPG*pat*/clpg*mat* and is therefore callipyge (phenotype) (Cockett et al., 1996). The second model is proposed to have two closely linked genes; one gene is maternally imprinted/paternally expressed and codes for a transacting suppressor of the other gene (Cockett et al., 1996). The callipyge phenotype occurs only when the second gene is expressed, such as a muscle growth enhancer. In the first model, muscular hypertrophy is caused by the lack of a gene product that limits muscle growth, and in the second model, muscular hypertrophy is caused by the presence of a product that promotes the growth of muscle.

The callipyge gene has been mapped to the distal end of the ovine chromosome 18 (Cockett et al., 1998). Freking et al. (1998) confirmed the proposed overdominance pattern and the position of the gene locus on chromosome 18. Another gene responsible for an increase in the loin eye area of lambs is the *Carwell* gene (Banks, 1997), which is allelic to callipyge and also originated in the Dorset breed. Expression of the *Carwell* gene is detected in live lambs only by ultrasonic scanning. At this time there is no evidence to suggest that the Carwell gene affects palatability, tenderness, fat thickness, or other performance characteristics.

ECONOMIC FACTORS

Market lambs with the callipyge phenotype have a higher DNA content in muscle apparent by 8 weeks of age in the loin eye (Lorenzen et al., 2000). A higher DNA content is likely due to an increase in satellite cell proliferation, resulting in an increased capacity of skeletal muscle to accumulate and maintain its protein. Lambs that exhibit the callipyge phenotype are superior to normal lambs in economically important traits, resulting in lower unit production costs for callipyge retail cuts (Busboom et al., 1998).

According to Busboom et al. (1998), the callipyge phenotype has the potential to decrease cost of lamb to consumers and increase profitability of the lamb industry. The cost of callipyge lamb with no added water and with added water would be reduced by 15.9% and 20.9%, respectively, compared to normal lamb. The value of callipyge and moisture-enhanced callipyge cuts from a 59-kg lamb would be 14.2% and 23.4% higher than for cuts from a normal lamb. The total production costs for a 59-kg lamb are 4% lower in callipyge lambs due to a 10% improved feed efficiency. Therefore, the callipyge gene should not affect production costs except for postweaning feed costs. Based on prices recorded in the January 16, 1998, issue of USDA *Weekly National Lamb Market Summary*, Busboom et al. (1998) calculated that callipyge cuts would be valued at $13.42 more than normal cuts, a 14.2% increase.

The use of one of several post-harvest treatment methods (see following section) is necessary for marketing the callipyge loin and rack (Carpenter et al., 1997; Koohmaraie et al., 1998). Busboom et al. (1998) estimated that the cost of tenderization and moisture enhancement would be accomplished for about $.10 per kg. Utilizing this estimate, the meat cost per kilogram of tenderized and moisture-enhanced callipyge leg, loin, rack, and shoulder containing 10% added water and ingredients would be decreased, thus, resulting in a 20.9% reduction in meat cost per kilogram compared to normal lambs (Busboom et al., 1998). An important factor to consider is the cost and effort required to implement post-harvest tenderization methods for callipyge lamb in individual packing operations. Without moisture enhancement or post-harvest tenderization treatment callipyge cannot be marketed. Pre-harvest approaches to increase meat tenderness involving management, nutrition, sex, and genetics have been examined to no avail.

PROCESSING FOR TENDERNESS

A number of post-harvest intervention strategies have been introduced to alleviate toughness of callipyge lamb. These strategies include: postmortem aging, electrical stimulation, combined freezing and thawing prior to aging (damages calpastatin, which reduces tenderness), calcium chloride injection (increases calpain activity, which increases tenderness), and the Hydrodyne process (physically disrupts the myofibril) (Solomon, 1998). It is interesting to note that Clare et al. (1997), reported that consumer panelists rated untreated callipyge leg chops 94% acceptable, loin chops 60% acceptable, and shoulder chops 89.4% acceptable in tenderness. After callipyge muscles were injected with calcium chloride, panelists rated 96.5% of leg chops, 85.4% of loin chops, and 93.5% of leg chops as acceptable in tenderness. Callipyge cuts injected with calcium chloride had a lesser degree of browning than callipyge control cuts from day 2 to day 5 in retail display (Clare et al., 1997). Therefore, calcium chloride injection can be used to decrease variation in palatability of the callipyge loin muscle.

A possible alternative to address negative quality of callipyge lamb carcasses might be the use of raw binder systems in restructured lamb. Berry et al. (1987) observed that size and shape of the particle used to manufacture the restructured product affected product texture. Numerous methods to reduce particle size of meat for use in restructured products include grinding, flaking, slicing, chunking, cubing, and fiberizing. Restructured meat products can be bound together through the formation of gels that are hot-set or cold-set. Conventional restructured meat products depend upon hot-set binding of meat proteins extracted with the combined effects of salt, phosphate and mechanical action. Such treatment limits the product to be marketed in either the precooked or frozen state, because binding is not very strong in the raw state. Several cold-set binding systems have been developed to meet the demand for restructured meat products that can be marketed in the raw, chilled state, having characteristics similar to cuts from intact muscles (Kuraishi et al., 1997). Advantages of cold-set over hot-set binding systems include less discoloration, which is common in hot-set products due to salt and phosphate, as well as oxidative rancidity.

Alginate, a polysaccharide extracted from brown seaweed, is added to many foods, including ice cream, pudding, salad dressing, and fruit juice and functions as a stabilizer, thickener, emulsifier, and gelling agent. Alginate forms a thermo-irreversible gel that can be used to bind diced pieces of meat together. Fibrimex™ is a blood-based binding system developed by Harimex in the Netherlands that can be used for binding comminuted and large pieces of meat. The binding mechanism is based on the blood clotting action between fibrinogen, thrombin, and transglutaminase, the stabilizing agent. Transglutaminase causes fibrin cross-linking between meat collagen and the fibrin gel (Boles and Shand, 1998). Fibrimex™ affects texture, binding, and yield of many protein-containing food products.

Boles and Shand (1998) studied the effects of alginate and Fibrimex binding systems on processing properties of restructured beef. The inside leg and round, mock tender, and clod muscles from young beef carcasses were obtained 4 to 5 days after slaughter. Steakettes were manufactured with either alginate or Fibrimex. Consumer panelists preferred steakettes manufactured with Fibrimex from inside round, mock tender and clod muscles over alginate products. When alginate was used to manufacture steakettes, muscle source had no effect on acceptability of steakettes (Boles and Shand, 1998). Researchers suggest that acceptable steakettes can be made with lower priced cuts when compared to steakettes made from more expensive cuts. The use and economics of raw binder systems have not been reported for callipyge lamb.

Currently, many packers are unwilling to purchase callipyge lambs (Sainz, 1996). The prolonged time required for aging-induced tenderization increases the amount of time carcasses remain in the packinghouse, which results in decreased storage efficiency. Sainz (1996) has stated that the “concern about tough meat has led the Superior Packing Company to reject any Callipyge lambs” and “at this time, callipyge lambs have no ready market”. Packers need to assess the costs and effort required for post-harvest tenderization and whether adding the procedure to their operation would be justified economically. Moisture-enhanced and restructured meat products have been accepted in other meat industries and other countries, but further studies are needed to determine whether consumers will accept moisture-enhanced or restructured callipyge lamb. Until researchers find ways to overcome the negative characteristic of toughness, producers have no outlet for the finished callipyge lamb.

SUMMARY AND CONCLUSIONS

The callipyge mutation results in a 20-38% increase in muscle mass or saleable meat in lambs. A complex breeding program is required to generate the necessary animals to produce callipyge lambs on a consistent and reliable basis. Callipyge lambs are superior to normal lambs in feed efficiency and dressing percentage, both of which are extremely desirable characteristics for producers and processors. However, the decreased tenderness of the loin eye is highly undesirable. Several techniques have been developed to overcome the tenderness problem, such as postmortem aging, electrical stimulation, combination of freezing and thawing prior to aging, calcium chloride injections, and hydrodynamic shock. Meat packers have been unwilling to undertake the added cost and time required for post-harvest tenderization of callipyge lamb. A possible approach might be the use of raw binder systems in restructured lamb products. Moisture enhancement to improve tenderness and restructured meat products from less desirable muscles have been accepted in other meat industries, but studies are needed to determine whether consumers will accept moisture-enhanced or restructured callipyge lamb. In conclusion, advantages of lambs expressing the callipyge phenotype in more muscular carcasses and increased quantities of major marketable cuts are useless if the industry fails to explore and adopt cost and time efficient techniques to improve tenderness.

REFERENCES

Banks, R. 1997. The meat elite project: Establishment and achievement of an elite meat sheep nucleus. Proc. Assoc. Adv. Anim. Breed. Genet. 12:598-601.

Berry, B. W., J. J. Smith, and J. L. Secrist. 1987. Effects of flake size on textural and cooking properties of restructured beef and pork steaks. J. Food Sci. 52:558-563.

Boles, J. A. and P. J. Shand. 1998. Effect of comminuted method and raw binder system in restructured beef. Meat Science 49:297-307.

Boles, J. A. and P. J. Shand. 1999. Effects of raw binder system, meat cut and prior freezing on restructured beef. Meat Science 53:233-237.

Busboom, J. R., T. Wahl, and G. D. Snowder. 1998. Economics of callipyge lamb production. J. Anim. Sci. 76:364 (Suppl. 1).

Carpenter, C. E., O. D. Rice, N. E. Cockett, and G. D. Snowder. 1996. Histology and composition of muscles from normal and callipyge lambs. J. Anim. Sci. 74:388-393.

Clare, T. L., S. P. Jackson, M. F. Miller, C. T. Elliott, and C. B. Ramsey. 1997. Improving tenderness of normal and callipyge lambs with calcium chloride. J. Anim. Sci. 75:377-385.

Cockett, N. E., S. P. Jackson, T. L. Shay, D. Nielsen, S. S. Moore, M. R. Steele, W. Barendse, R. D. Green, M. Georges. 1994. Chromosomal localization of the callipyge gene in sheep (*Ovis aries*) using bovine DNA markers. Proc. Natl. Acad. Sci. 91:3019-3023.

Cockett, N. E., S. P. Jackson, T. L. Shay, F. Farnir, S. Berghmans, G. D. Snowder, D. M. Nielsen, M. Georges. 1996. Polar overdominance at the ovine *callipyge* locus. Science 273:236-238.

Cockett, N. E., T. L. Shay, S. Berghmans, S. P. Jackson, G. D. Snowder, C. Carpenter, and M. Georges. 1998. The callipyge phenomenon: evidence for unusual genetic inheritance. J. Anim. Sci. 76:363 (Suppl. 1).

Duckett, S. K., T. A. Klein, M. V. Dodson, and G. D. Snowder. 1998. Tenderness of normal and callipyge lamb aged fresh or after freezing. Meat Science 49:19-26.

Duckett, S. K. 2000. Subject: Carcass and meat quality of callipyge lambs. http://www.uidaho.edu/~sduckett/extclpg.htm. Accessed Nov. 27, 2000.

Freking, B. A., J. W. Keele, C. W. Beattie, S. M. Kappes, T. P. L. Smith, T. S. Sonstegard, M. K. Nielsen, and K. A. Leymaster. 1998. Evaluation of the ovine *callipyge* locus: I. Relative chromosomal position and gene action. J. Anim. Sci. 76:2062-2071.

Freking, B. A., and K. A. Leymaster. 1998. Effect of callipyge (CLPG) genotypes on growth, carcass, and reproduction traits. J. Anim. Sci. 76:363 (Suppl. 1).

Jackson, S. P., R. D. Green, and M. F. Miller. 1997. Phenotypic characterization of Rambouillet sheep expressing the Callipyge gene: I. Inheritance of the condition and production characteristics. J. Anim. Sci. 75:14-18.

Koohmaraie, M., S. D. Shackelford, T. L. Wheeler, S. M. Longerran, and M. E. Doumit. 1995. A muscle hypertrophy condition in lamb (callipyge): characterization of effects on muscle growth and meat quality traits. J. Anim. Sci. 73:3596-3607.

Koohmaraie, M., S. D. Shackelford, and T. L. Wheeler. 1998. Muscle growth, carcass composition, and meat tenderness of callipyge lamb: A review. J. Anim. Sci. 76:363 (Suppl. 1).

Kuraishi, C., J. Sakamoto, K. Yamazaki, Y. Susa, C. Kuhara, and T. Soeda. 1997. Production of restructured meat using microbial transglutaminase without salt or cooking. J Food Sci. 62:488-490.

Leroy, P. L. 2000. Subject: Texel Double Muscling. http://www.ulg.ac.be/fmv/texeldm/. Accessed Nov. 27, 2000.

Leymaster, K. A., and B. A. Freking. 1998. Genetic aspects of callipyge implementation by the sheep industry. J. Anim. Sci. 76:364 (Suppl. 1).

Lorenzen, C. L., M. Koohmaraie, S. D. Shackelford, F. Jahoor, H. C. Freetly, T. L. Wheeler, J. W. Savell, and M. L. Fiorotto. 2000. Protein kinetics in callipyge lambs. J. Anim. Sci. 78:78-87.

Sainz, R. D. 1996. http://animalscience.ucdavis.edu/highlights/fall1996/fall1996_04.htm

Sainz, R. D. 2001. Callipyge meat a tough sell. *California Agriculture* 55(6):23.

Shelley, J. M., J. D. Kemp, W. Deweese, D. D. Kratzer, and D. G. Ely. 1970. Effect of castration, slaughter weight, and testosterone on lamb carcass composition and palatability. J. Animal Sci. 31:189 (Abstract).

Solomon, M. B. 1998. The callipyge phenomenon: challenges and opportunities: toughness intervention methods. J. Anim. Sci. 76:364 (Suppl. 1).

GLOSSARY OF TERMS

Adductor Muscle: Muscle of the inside round that draws toward the median line of the body or toward the axis of an extremity (Gluteus Medius, Gluteus Minimus).

Allele: One of two or more alternative forms of a single gene locus.

Autosome: All chromosomes other than the sex chromosomes.

Biceps femoris Muscle: Bottom round muscle.

Calpain: An intracellular cysteine protease synthesized as an inactive proenzyme. Activation occurs by autocatalytic cleavage in the presence of high calcium concentrations. Plays a major role in muscle growth and development and post mortem tenderization.

Calpastatin: A specific endogenous inhibitor of protein.

Carwell Gene: Originally identified in Australian Poll Dorsets, is a simple autosomal dominant mutation located on the telomeric end of chromosome 18, results in a 7% increase in longissimus muscle weight, without effect on other muscles or meat quality. Detectable in live lambs only by ultrasonic scanning.

Cutability: Refers to the amount of closely trimmed retail cuts that can be obtained from The leg, loin, rack, and shoulder; yield grade.

Dressing Percentage: The carcass weight of a meat animal expressed as the percentage of the live weight.

Dystocia: Difficult birth.

Fast-twitch Glycolytic Muscle Fibers: Characterized as white muscle that is fast fatigue, fast contracting. Contains less myoglobin than slow-twitch muscle fibers. Anaerobic. Predisposed muscle to quality defects.

Fatness: (a) **Subcutaneous:** Fat deposited over the muscular part of the body and just beneath the skin.

(b) Intermuscular: (Seam Fat) Fat that is deposited between individual muscles.

(c) Intramuscluar: (Marbling) Fat that is deposited between the muscle bundles within the perimyseal connective tissue.

(d) Perinephric: (Kidney Fat) Fat that surrounds the kidney and forms a deposit on the inner side of the loin.

Hyperplasia: Prenatal growth accomplished by accumulation of cell products, responsible for an increase in cell number.

Hypertrophy: Postnatal growth accomplished by mitotic cell division, responsible for an increase in cell size.

Imprinting: An allele-specific reversible epigenetic modification dependent on the parental origin of the allele, which can cause functional differences in development. Growth and development are among the traits affected by gametic imprinting.

Infraspinatus Muscle: Function to stabilize the shoulder, abduct and externally rotate foreleg. It originates on the dorsal surface of the scapula, and on the spine of the scapula, and inserts on the posterior aspect of the humerus. Occupies the infraspinous fossa.

Myofibrils: Long cylindrical cytoskeletal elements that extend the length of the cell, contain actin and myosin that contract after death.

Mutation: A physical change in the chromosome or a biochemical change in the codons that make up genes, may be dominant or recessive.

Phenotype: The appearance of the animal or one of its traits; the way an animal appears or behaves as determined in part by the genotype.

Polar Overdominance (Maternal): Only heterozygous offspring inheriting a mutation from their dam express the resulting phenotype.

Polar Overdominance (Paternal): Only heterozygous offspring inheriting a mutation from their sire express the resulting phenotype.

Satellite Cell: Small mononucleated cells that reside between the sarcolemma and plasma membrane. Retains the ability to grow and divide. Accommodates postnatal growth and muscle repair.

Semimembranosus Muscle: The medial muscle of the group of extensor muscles of the hip. Located on the medial side of the femur.

Slow-twitch Oxidative Muscle Fibers: Characterized by dark muscle that is slow contracting. Contains myoglobin and can use fat for energy. These fibers are smaller than 'white' fibers.

Supraspinatus Muscle: Function to stabilize shoulder, abduct and externally rotate foreleg. Originates above the spine of the scapula and inserts on the head of the humerus. Occupies supraspinous fossa.

Thoracic Muscle: Functions principally in extension, adduction, internal rotation, and depression of the humerus.