BIOTECHNOLOGY AND ANIMAL PRODUCTS: PROBABLE EFFECTS ON FAT COMPOSITION

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Summary

Our current concept of biotechnology, as it relates to the production of meat and meat products, revolves around the use of repartitioning agents and the development of transgenic livestock species. The profound effectiveness of repartitioning agents (the somatotropins and ß-adrenergic agonists) has provided scientists with a unique opportunity to investigate the cellular and physiological regulation of muscle and adipose tissue growth and development. Cloning of the gene encoding the somatotropin (growth hormone; GH) also has led to the development of GH-transgenic livestock. These aspects of biotechnology, as well as their effects on fat composition, are the primary focus of this presentation. Although there are very real differences across species and even among cell types in the effects of repartitioning agents, some general statements can be made about their mode of action on muscle and adipose tissue. There is convincing evidence that two independent processes occur in the muscle of GH-transgenic animals and livestock treated with repartitioning agents: stimulation of myofibrillar protein synthesis, either at the transcriptional or translational level; and depression of myofibrillar protein degradation. Similarly, some general effects of repartitioning agents have been documented for adipose tissues. Chronic exposure of cattle to ß-adrenergic agonists results in reductions in adipocyte volume in several depots, and indirect evidence suggests depression of preadipocyte hyperplasia and (or) requirement in growing lambs chronically exposed to these compounds. Acute effects of ß-adrenergic agonists include stimulation of lipolysis and inhibition of lipogenesis, which also is seen with the chronic administration of the somatotropins. These effects ultimately result in the production of more lean tissue containing less total fat. The concomitant reduction in saturated fatty acids and cholesterol apparently has no negative effect on the processing characteristics of the meat from transgenic animals or from animals treated with repartitioning agents.

Introduction

Considerable progress has been made recently in understanding the processes regulating the growth and development of muscle and adipose tissue of livestock species. This has been facilitated by the discovery of several compounds (known collectively as repartitioning agents) that exert dramatic effects on carcass composition. The family of repartitioning agents includes the synthetic ß-adrenergic agonists, which structurally resemble the catecholamine family. Gross effects on carcass composition of the most commonly used ß-adrenergic agonists, clenbuterol, cimaterol and ractopamine, have been well documented.

Included in the family of repartitioning agents are the somatotropins. The somatotropins include porcine somatotropin (pST) and bovine somatotropin (bST). These endogenously produced (hence naturally occurring) growth modifiers also are known as growth hormones (GH). Until recently, the somatotropins had to be obtained from the pituitaries of animals. More recently, growth hormone genes have been cloned, and the somatotropins now are produced in large quantity by recombinant DNA methodologies. This has provided enough of the hormone so that it can be tested in livestock. Scientists now know that the injection of bST into dairy cows increases milk production, whereas treatment of pigs with pST increases the production of lean meat.

Repartitioning agents are important not only in that they are powerful tools with which to manipulate adipose tissue and muscle metabolism, but also because they have profound effects on carcass composition. Hence,

attempting to understand how repartitioning agents exert their effects provides us with the insight to predict how they will affect meat quality. Our understanding of these processes has been facilitated by the development and characterization of transgenic livestock (especially transgenic pigs), in which the somatotropin gene from one species is integrated into the genome of another species.

Repartitioning Agents and Carcass Characteristics

No discussion of repartitioning agents would be complete without at least a cursory description of the effects they have on carcass composition. Effects on the carcass traits of livestock species were first described for clenbuterol, a synthetic analog of epinephrine. Clenbuterol increased dressing percentage, loin-eye area and overall muscle deposition in wether lambs (Baker et al., 1984; Hamby et al., 1986) and in cattle (Ricks et al., 1984; Miller et al., 1988; Schiavetta et al., 1990). Cimaterol, which is structurally similar to clenbuterol, has similar effects in lambs (Beermann et al., 1987; Kim et al., 1987; Wang and Beermann, 1988), steers (Hanrahan et al., 1986), poultry (Dalrymple et al., 1984) and swine (Jones et al., 1985). Ractopamine, another phenethanolamine possessing ß-adrenergic agonist activity, appears to be one of more effective agonists of muscle growth in swine (Anderson et al., 1987; Bergen et al., 1989). Like the ß-adrenergic agonists, the injection of pST into pigs markedly increases the rate of muscle growth and decreases the rate of fat accretion (Campbell et al., 1990).

Cloning of the growth hormone gene was the initial step in producing transgenic animals. Once cloned, the GH-gene was packaged with a strong promoter and was microinjected into fertilized eggs (zygotes) where it became incorporated into genomic DNA. These GH-transgenic animals express high levels of growth hormone, and thus grow similarly to growth hormone-injected animals. Thus, introduction of the porcine growth hormone fusion gene into pigs increased overall growth rate (Vize et al., 1988). The biochemical, cellular and systemic bases for the observed carcass effects have been the subject of intense interest in recent years.

Repartitioning Agents and Muscle Growth

Muscle Fiber Types. Muscle hypertrophy is one of the most consistently observed effects of the administration of repartitioning agents. There are two major types of muscle fibers occurring in skeletal muscle, either of which can undergo hypertrophy. Hamby et al. (1986) reported that in lambs fed clenbuterol for 40 d, longissimus muscle strips incubated in vitro displayed greater total glucose utilization and rates of glycogen synthesis, indicating hypertrophy of type II fibers relative to controls. Correspondingly, in heifers fed clenbuterol for 50 d, longissimus muscle hypertrophy was brought about by an increase in the diameter of type II fibers only (Miller et al., 1988). Similar results were obtained in the semitendinosus and longissimus muscles of lambs fed clenbuterol (Kim et al., 1987). However, in wether lambs fed cimaterol for 6 or 12 wk, semitendinosus muscle hypertrophy was brought about by a 30% increase in the diameters of both type I and type II myofibers (Beermann et al., 1987). Young steers fed clenbuterol early in the finishing phase dem-onstrated similar increases in diameter of both SDH-negative and SDH-positive myofibers (Garcia et al.,1988; Figure 1).

Similar effects have been observed in growing pigs treated with pST (Solomon et al., 1988). In addition, pST caused the transformation of intermediate fibers (type II, SDH positive) to white fibers (type II, SDH negative). Moreover, pST treatment caused the production of giant fibers (Solomon et al., 1988), which are abnormally large fibers with staining characteristics of both type I and type II fibers. Because the repartitioning agents generally increase either the percentage or the size of type II fibers, which inherently contain less lipid than type I fibers, the overall effect of these compounds would be to reduce the total lipid content of the muscles and/or carcass. This has been demonstrated in sheep (Baker et al., 1984; Hamby et al., 1986) and pigs (Campbell et al., 1990).

Myofibrillar Protein Synthesis. Investigators have demonstrated a stimulatory effect of repartitioning agents on protein synthesis. Ractopamine increased the protein fractional synthetic rate in pigs (Bergen et al., 1989). This compound has also been reported to cause an increase in nitrogen retention in ovine (Kim et al., 1989) and swine muscle in vivo (Anderson et al., 1987). Increased uptake of α-amino nitrogen, a reliable index of elevated rates of protein synthesis, has been observed in the hindlimbs of steers fed clenbuterol (Eisemann et al., 1988) and clenbuterol increased whole body protein synthesis in lambs (Claeys et al., 1989). Similarly, somatotropin administration to pigs increased the rate of carcass protein accretion (Campbell et al., 1990).

Myofibrillar Gene Expression. There is convincing evidence that repartitioning agents can increase muscle hypertrophy by direct effects on the transcription of genes encoding myofibrillar proteins, independently of effects on satellite cells. Cimaterol-induced hypertrophy of the semitendinosus muscle in lambs was elicited with an associated increase in protein and RNA content of 30% and 35%, respectively (Beermann et al., 1987).

An increase in the expression of the gene that encodes both myosin light chain 1 and myosin light chain 3, evidenced by an increase in the production of the mRNA for these proteins, was observed in muscle of steers fed ractopamine (Smith et al., 1989). Additionally, Garcia et al. (1988) reported an increased concentration of α-actin mRNA in clenbuterol-treated steers (Figure 2). A recent report by Young et al. (1990) clearly demonstrated that chicken muscle cell cultures treated with cimaterol exhibited increased rates of myosin heavy chain synthesis, concomitant with an increased concentration of myosin heavy chain mRNA. It therefore is likely that increased transcription of genes encoding myofibrillar proteins is a mechanism by which repartitioning agents exert their effects in muscle.

Myofibrillar Protein Degradation. Decreased protein degradation is another mechanism by which net protein accretion can be achieved by repartitioning agents. If protein degradation is decreased by the administration of repartitioning agents, then it likely is elicited by decrease in the activity of one or more of the enzymes responsible for myofibrillar protein degradation. These enzymes include the calcium-dependent proteases and the lysosomal proteases, or cathepsins. In lambs (Forsberg et al., 1987) and chickens (Morgan et al., 1989) treated with cimaterol, catheptic enzyme activities were reduced relative to control activities (Figure 3).

The calcium-dependent proteases also appear to be sensitive to treatment with repartitioning agents. Wang and Beermann (1988) reported decreased calcium-dependent protease activities in longissimus muscle of sheep fed cimaterol. Similar results were observed in muscles of cimaterol-fed rabbits (Forsberg et al., 1989), as were reductions in calpastatin, the protein that suppresses the calcium-dependent proteases in situ. It is likely that the reduction in endogenous proteases is the basis for the decreased tenderness of meat from animals treated with ß-adrenergic agonists (Figure 4) or pST (Solomon et al., 1988). Hamby et al. (1986) first reported that clenbuterol treatment of lambs caused nearly a two-fold increase in Warner-Bratzler shear force of chops from the treated lambs. More recently, Morgan et al. (1989; Figure 4) and Fiems et al. (1990) demonstrated decreased tenderness in meat from cimaterol-treated chickens and bulls, respectively. It should be noted that reductions in tenderness have not been reported for meat from pigs treated with ß-adrenergic agonists, which is consistent with the lack of effect of these compounds on muscle proteases in porcine muscle (Bergen et al., 1989), whereas pST treatment does decrease the tenderness of pork (Solomon et al., 1990). Although repartitioning agents consistently increase the rate of muscle hypertrophy in animals, it is apparent that the cellular/biochemical basis for the effects of these compounds depends on the species as well as the particular type of hormone that is used.

Repartitioning Agents and Adipose Tissue Growth

In addition to increasing the rate of muscle growth, repartitioning agents typically reduce total carcass fat, whether measured as ether-extractable fat of the muscle, percentage dissectable carcass fat, USDA yield grade,

or subcutaneous fat thickness. The only documented increase in carcass fatness in animals treated with repartitioning agents was for broiler cockerels injected with chicken growth hormone (Cogburn et al., 1989).

Reduced carcass adipose tissue content could be the result of increased rates of lipolysis, decreased fatty acid and/or triglyceride biosynthesis, reduced adipocyte proliferation/recruitment, or some combination of these events. Additionally, these processes could be affected directly, or their response to repartitioning agents could merely represent the reduction in energy available for fat deposition as animals are actively accreting muscle in response to treatment. Investigations of the effects of repartitioning agents on lipolysis and lipogenesis have been of two general types: those in which tissue from chronically treated animals was incubated in vitro, and the resultant metabolic products measured; and those in which the repartitioning agent was added directly to the incubation media in order to measure acute effects of the hormones.

Adipose Tissue Metabolism – Chronic Administration of Repartitioning Agents. There have been few published reports of the effects of chronic exposure to repartitioning agents on adipose tissue lipogenesis in livestock species. Lipogenesis from acetate in subcutaneous adipose tissue was reduced in heifers fed clenbuterol for 50 d (Miller et al., 1988). Basal lipolysis was unaffected in adipose from the heifers that had been fed clenbuterol (Miller et al., 1988). Ractopamine also reduced adipose tissue lipogenesis in growing swine (Merkel et al., 1987). Similarly, fatty acid synthesis in porcine adipose tissue was reduced by the administration of pST to pigs (Kramer et al., 1990). This is in contrast to studies done with growing sheep in which no change in, or an increased rate of, lipogenesis was seen in subcutaneous adipose tissue after the long-term administration of clenbuterol (Coleman et al., 1988) or cimaterol (Hu et al., 1988).

Adipose Tissue Metabolism – Acute Administration of ß-adrenergic Agonists. Lipogenesis and lipolysis in rodent adipose tissues are especially sensitive to ß-adrenergic agonists, and are markedly inhibited and stimulated, respectively, in response to agonist challenge in vitro. Correspondingly, increased rates of lipolysis (Thornton et al., 1985; Peterla et al., 1987), and decreased lipogenesis (Peterla et al., 1987) were observed in ovine adipose tissue incubated in vitro with ß-adrenergic agonists. However, when incubated with clenbuterol in vitro, lipogenesis in adipose tissue from steers did not differ from lipogenesis in control adipose tissue (Miller et al., 1989). Moreover, acute administration of adipose tissues with somatotropins generally does not affect lipogenesis or lipolysis.

Repartitioning Agents and Adipose Tissue Cellularity. In cattle, the reductions in adipose tissue growth caused by the feeding of ß-adrenergic agonists is accompanied by a reduction in adipocyte size. This has been demonstrated for bovine subcutaneous, perinephric and interfascicular adipose tissues (Miller et al., 1988, 1989; Schiavetta et al., 1990), and usually resulted in reduced subcutaneous fat thicknesses, marbling scores and estimated kidney-pelvic-heart fat percentages. However, for growing lambs, in which the effects of ß-adrenergic agonists on subcutaneous fat thickness typically are the most pronounced (30-to-40% reductions), either a small decrease in subcutaneous adipocyte size (Hu et al., 1988) or an actual increase in adipocyte diameter (Coleman et al., 1988) were observed. Thus, it appears that these synthetic catecholamines may in part depress adipose tissue accretion by restricting either preadipocyte proliferation or recruitment. Feeding clenbuterol to young steers for 50 d did not affect 9-10-11th rib adiposity (Schiavetta et al., 1990; Figure 5). However, subsequent withdrawal from the compound for 78 d caused a burst of apparent hyperplasia, in which the number of measurable 9-10-11th rib subcutaneous adipocytes increased over 50% in the previously treated animals (Schiavetta et al., 1990; Figure 5).

Repartitioning Agents and the Lipid Composition of Meat. As indicated above, repartitioning agents reduce the extractable lipid content of muscle and decrease adipocyte volume. Both of these effects should reduce the amount of saturated fatty acids and cholesterol, which are the primary components of storage lipids. In contrast, treatment with repartitioning agents would be expected to enrich the proportion of polyunsaturated fatty acids

which, as components of membranes, would be less affected by hormonal treatment. Hu et al. (1988) first reported that feeding cimaterol to sheep increased the proportion of unsaturated fatty acids in their adipose tissues (Figure 6). Similarly, carcasses of transgenic pigs contained 38-51% less total lipid than carcasses from control pigs, with most of the reduction observed in the saturated and monounsaturated fatty acid components of the lipid (Solomon et al., 1990). This is consistent with repartitioning agents causing more pronounced reductions in storage lipids than in membrane lipids.

In pigs fed ractopamine, longissimus muscle cholesterol content was reduced from 57.8 to 53.1 mg per 100 grams of muscle (McKeith et al., 1990). However, Lentsch et al. (1990) reported that, while pST reduced the lipid content of porcine longissimus muscle (from 2.9% to 1.8%), it had no effect on muscle cholesterol content. Because there is approximately 1 mg cholesterol per gram of extractable lipid (Sweeten et al., 1990), the reduction in lipid reported by Lentsch et al. (1990) would result in only a 1.1 mg reduction in cholesterol (per 100 grams of muscle). This small difference in cholesterol is beyond our current level of detection.

Acceptability of Meat from Animals Treated with Repartitioning Agents. The improvements in carcass characteristics elicited by the administration of repartitioning agents are meaningless if the meat produced from these animals suffers losses in palatability or acceptability by the consumer. To date, it is not possible to feed meat from animals treated with ß-adrenergic agonists to humans. However, mechanical measures, such as shear force, have indicated that meat from cattle and sheep consuming ß-adrenergic agonists tends to be less tender; the same has been demonstrated for pork from pST-treated pigs. These effects appear to be species-related, because ß-adrenergic agonists appear to have no effect on tenderness of meat from pigs.

The reduction in fat, as well as the alteration in the fatty acid and cholesterol content of meat caused by the somatotropins also would be expected to influence consumer acceptability and processing characteristics of the meat. However, cooked pork chops from pigs treated with pST rated as highly as control chops when evaluated by consumers (Prusa et al., 1990). Springiness and firmness, as evaluated by a trained taste panel, increased as a result of pST treatment in frankfurters made with pork from treated pigs (Reagan et al., 1990). Additionally, overall palatability was greater for the frankfurters from the treated pigs than from frankfurters from control pigs (Reagan et al., 1990).

From the information that currently is available, it would appear that repartitioning agents have profound effects on the composition of meat, and we are beginning to understand the biochemical and cellular bases for these changes. While there may be some problems associated with the tenderness of meat from treated animals, the reduction in saturated fatty acids and cholesterol elicited by repartitioning agents apparently does not detract from the palatability of meat and meat products, and may result in a more healthful meat product.

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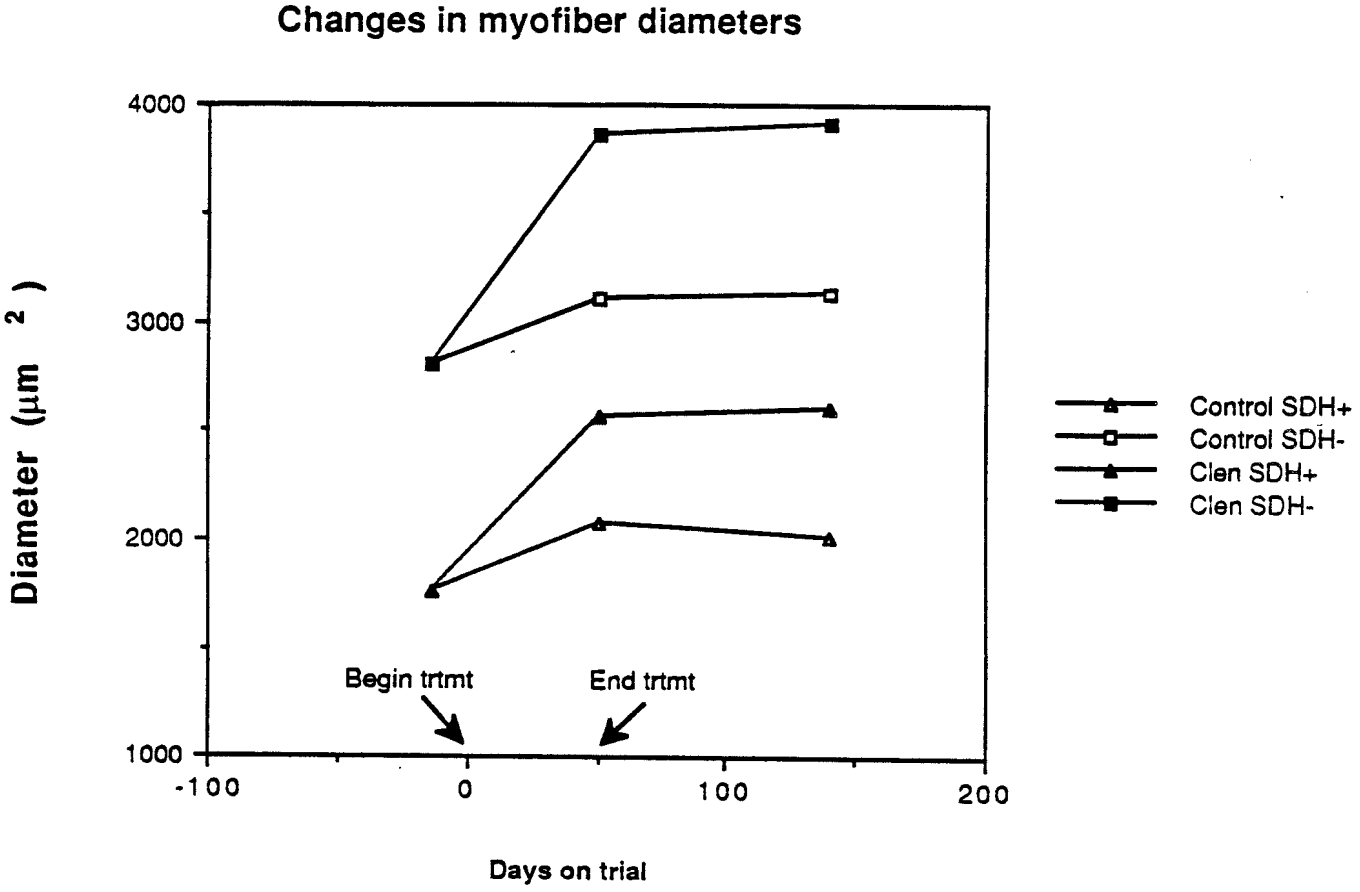

Figure 1. Changes in myofiber diameters of succinic dehydrogenase negative (SDH -; "white") and succinic dehydrogenase positive (SDH +; "red") myofibers from the longissimus muscle of Angus steers. Cattle were fed 7 mg clenbuterol per d for 50 d, after which clenbuterol was removed from the diet and the steers were fed for an additional 78 d. Eight steers were slaughtered at d 0 to serve as a baseline group, and 8 each control and clenbuterol-fed steers were slaughtered at d 50 and d 128 (from Garcia et al., 1988 and Schiavetta et al., 1990).

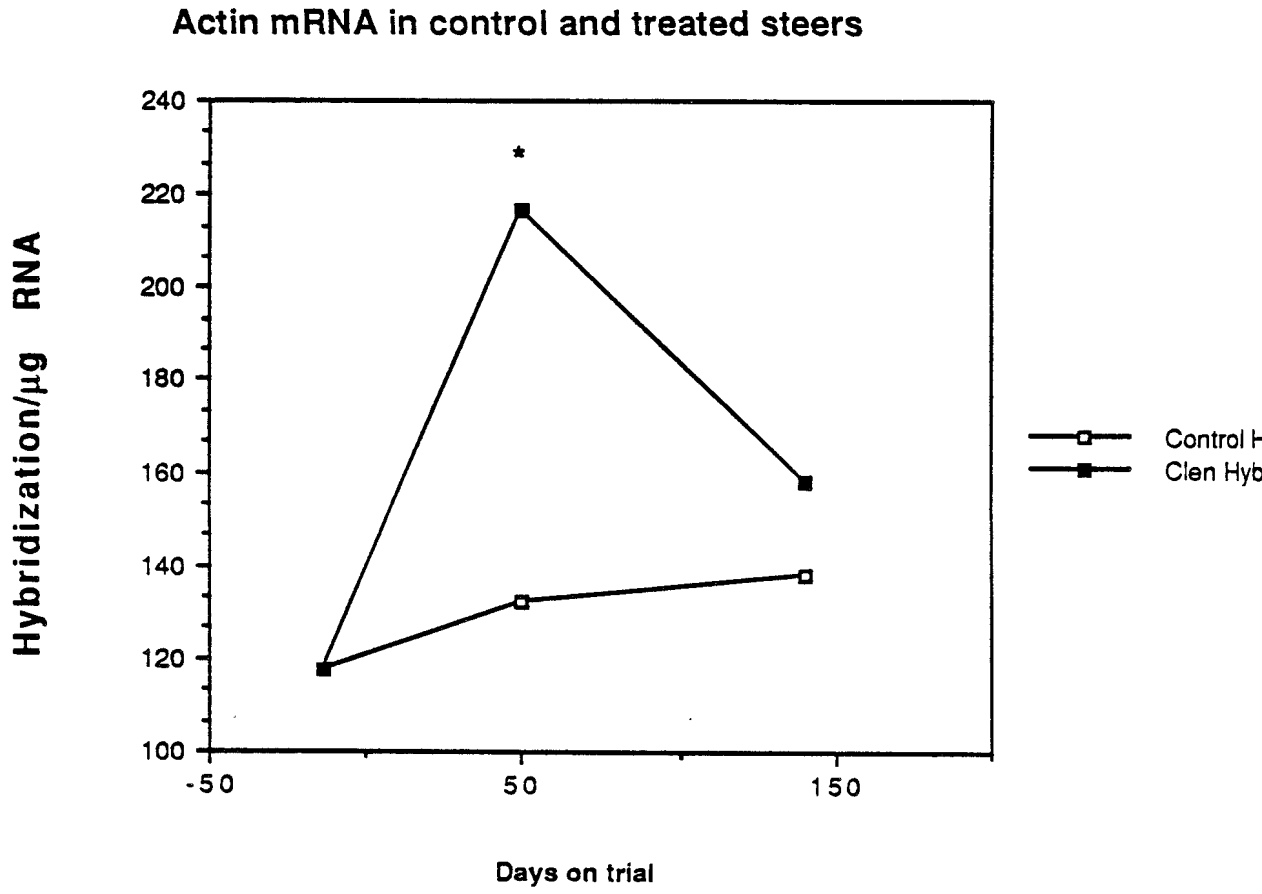

Figure 2. Hybridization of cDNA for *D. melanogaster* α-actin to longissimus muscle RNA from control and clenbuterol-fed Angus steers. Experimental design as described in Figure 1. Data are expressed as arbitrary optical density units taken from laser densitometry scans of slot blot autoradiograms of 5 µg total RNA. Clenbuterol increased ($P < .05$) α-actin mRNA at d 50 (from Garcia et al., 1988).

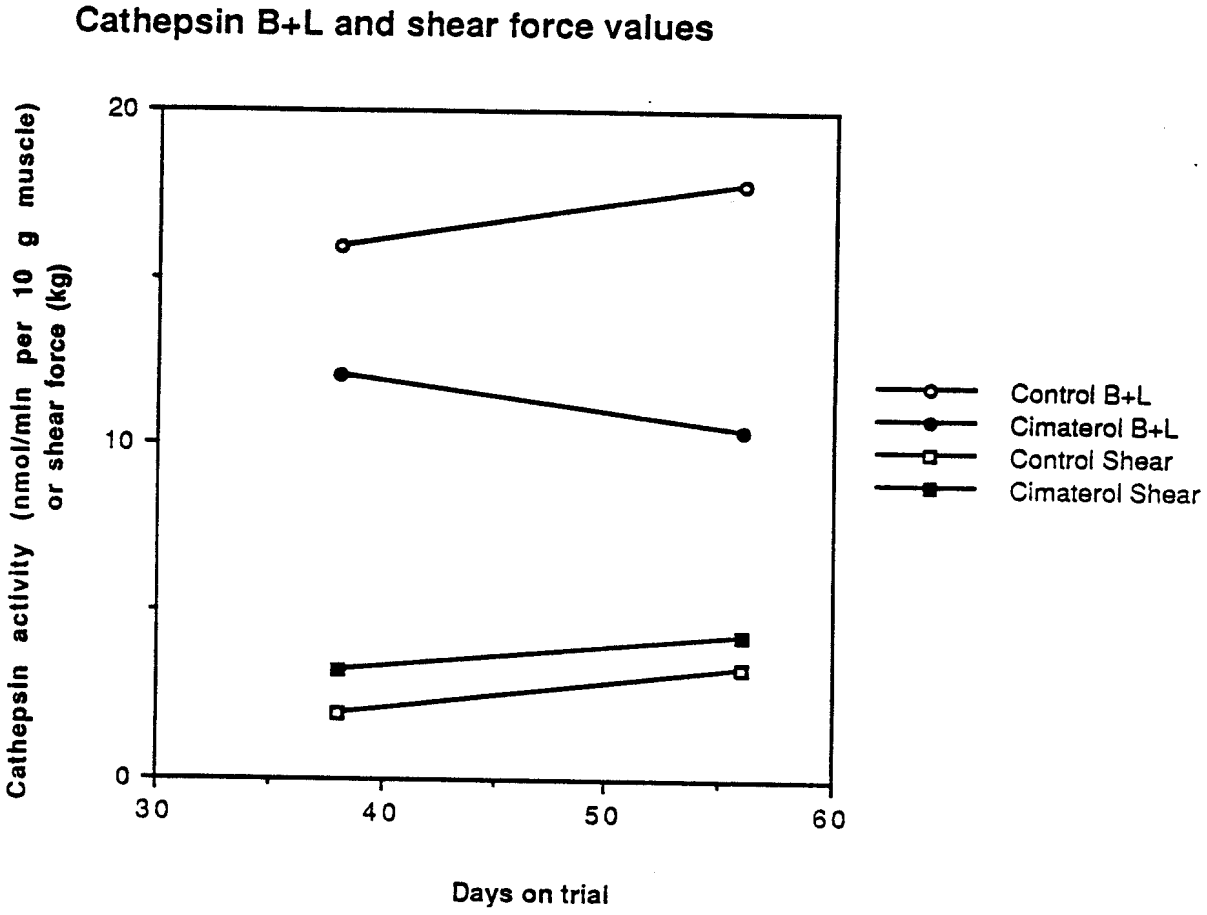

Figure 3. Cathepsin B + L and shear force values for muscle from broiler chickens fed cimaterol. Cimaterol treatment significantly increased shear force values and reduced catheptic enzyme activity at both treatment intervals (figure derived from data of Morgen et al., 1989).

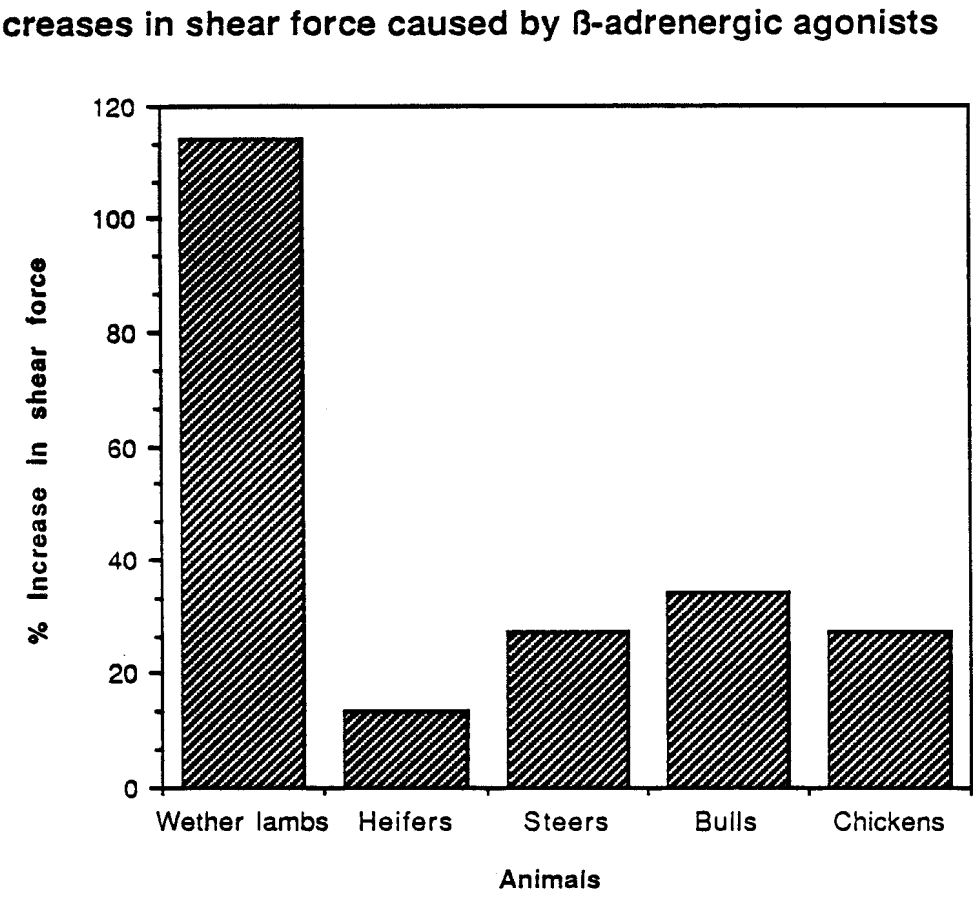

Figure 4. Effects of ß-adrenergic agonists on shear force values of meat from wether lambs (Hamby et al., 1986), heifers (Miller et al., 1988), steers (Schiavetta et al., 1990), bulls (Fiems et al., 1990) and chickens (Morgan et al., 1989). Data are expressed as percentage change from control for clenbuterol-fed lambs, heifers and steers and cimaterol-fed bulls and chickens. Significant increases in shear force were observed in all experiments, possibly reflecting a reduction in the activity of endogenous proteases with ß-adrenergic agonist treatment.

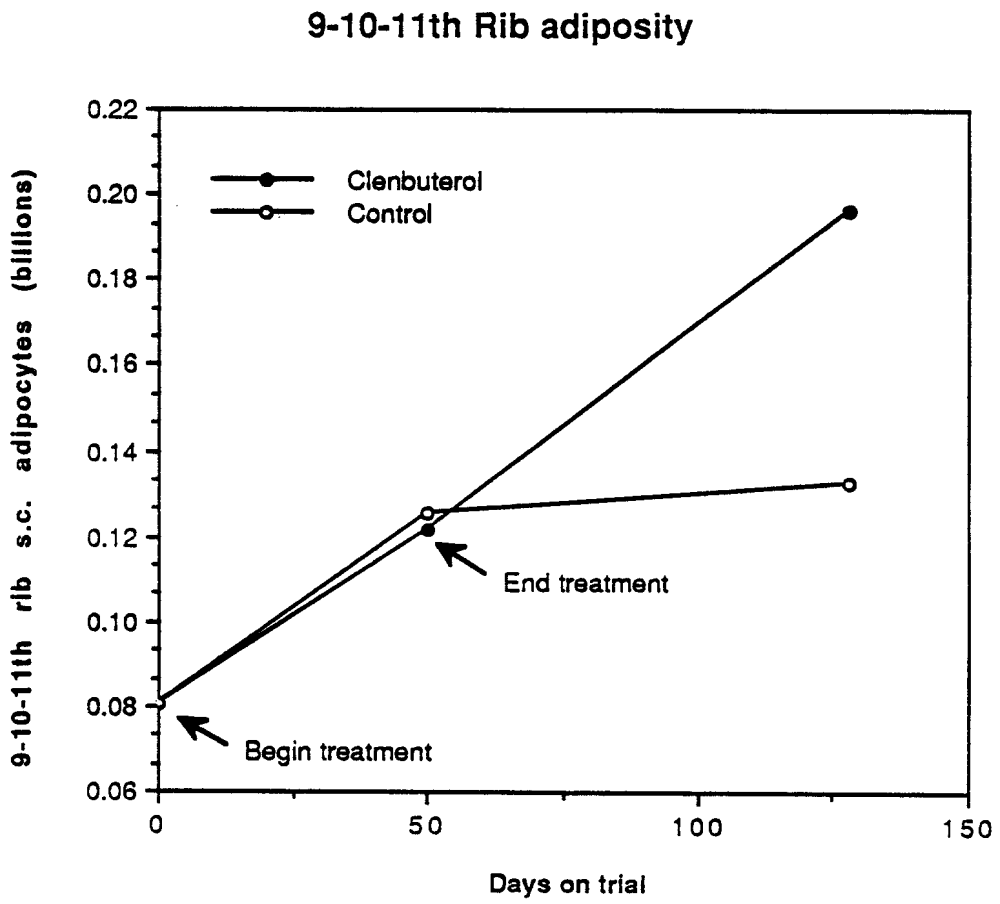

Figure 5. Adiposity of the 9-10-11th rib subcutaneous adipose tissue of Angus steers fed clenbuterol. Clenbuterol treatment for 50 d did not affect the total number of rib subcutaneous adipocytes. However, upon withdrawal from treatment, the number of subcutaneous adipocytes in the rib section of the treated group increased significantly (from Schiavetta et al., 1990).

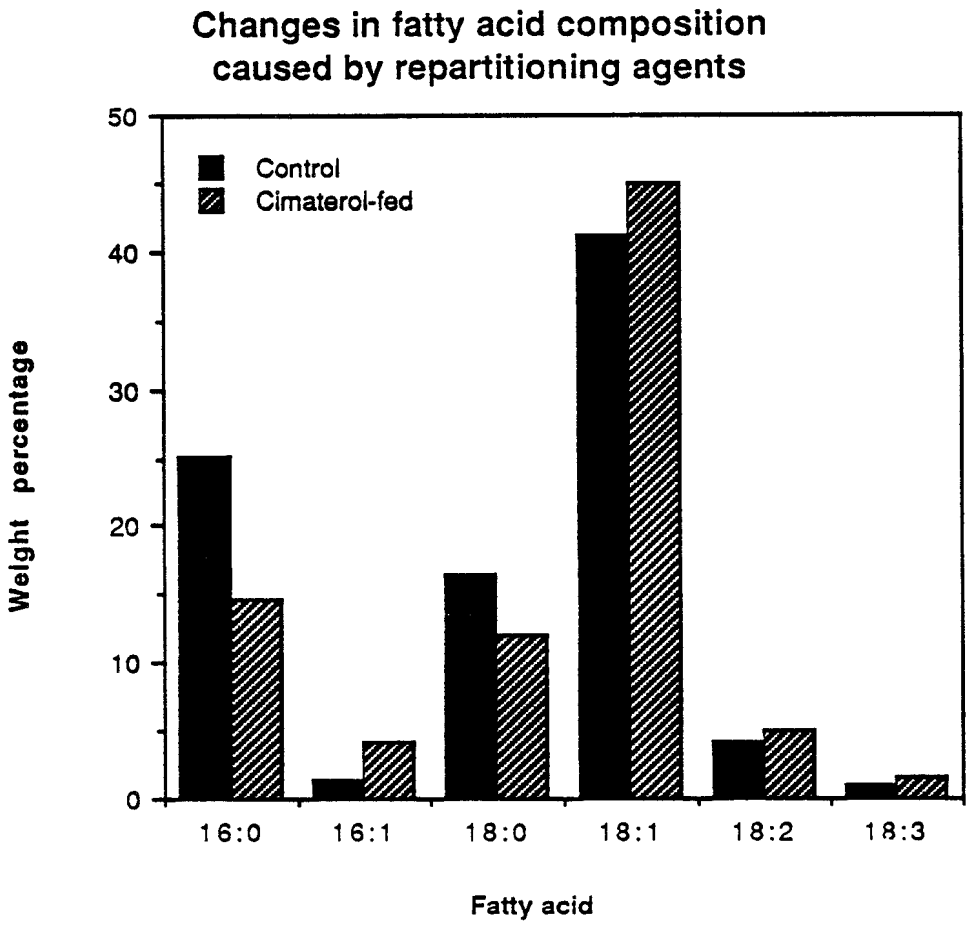

Figure 6. Fatty acid composition of subcutaneous adipose tissue of lambs fed 0 or 5 mg/kg diet for 28 d. Cimaterol significantly increased the weight percentages of all of the unsaturated fatty acids except linoleic acid (18:2), and decreased the saturated fatty acids (from Hu et al., 1988).