Genetic variation in protein metabolism and implications for variation in efficiency of growth

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Summary

Variation in protein metabolism accompanies genetic selection for a wide range of traits including growth of lean tissue, wool and possibly residual feed intake. This variation is observed at the level of protein and amino acid kinetics in response to nutrient supply in major tissues. There are associated effects on cellular development, endocrine secretion, hormonal action at the tissue level, enzyme activity within tissues and supply of nutrients from digested feed, which would be expected to lead to change in protein metabolism throughout the organism. Indeed, there are associations between rate of protein metabolism in muscle *in vivo* which affect the eating quality of meat. Despite evidence at the tissue level, at the whole body level variation in efficiency of protein deposition due to genetic selection is not readily observed in farm animals. This suggests there may be a conceptual or methodological problem in our approach in protein and energy nutrition of the whole animal.

Introduction

There is increasing interest in identifying cattle (and other stock) which differ in their capacity to use feed for maintenance and gain. Such an idea presents difficulty to our nutritional models in which variation between input and output are principally associated with properties of the feed, rather than arising from interactions between animal and feed. Evidence for genetic variation in processes which could, at least in theory, affect efficiency of use of nutrients is presented here. It could have a profound impact on how we construct systems which relate nutrient supply to animal performance in the future.

In this short review, I will present evidence of genetic variation in partitioning of protein between organs within the body, protein kinetics, and associated energy cost in muscle, and indicate that there may even be genetic variation at the levels of digestion of feed and amino acid supply per unit of feed digested. The issue of related differences in body composition between selected lines of cattle will be addressed elsewhere in these proceedings (Richardson *et al*. 1999).

Genetic variation in components of protein turnover—evidence from studies of animals from selection lines

Single character phenotypic selection of Merino sheep for (W+) and against (W–) weight at weaning (Pattie and Williams, 1966) has resulted in lines of sheep which differ in feed intake, growth rate, mature size and relative proportions of lean body mass to wool (Thompson *et al*. 1985). Although these lines of animals differ in intake and growth rate they do not differ in the amounts of digestible organic matter utilised for maintenance or gain (Pattie and Williams 1967; Herd *et al*. 1993), but they do differ in the efficiency of use of feed for wool

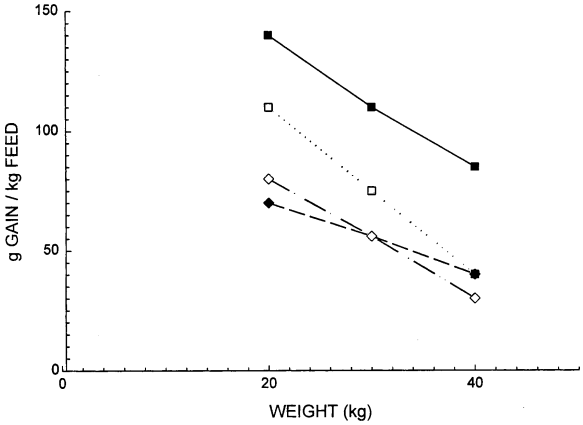

Figure 1 Effect of genetic selection for (W+) and against (W–) weaning weight in Merino sheep on utilisation of feed intake for lean and fat gain. Solid squares = lean gain g/kg feed eaten in W+, open squares = lean gain in W–, solid diamonds = fat gain g/kg feed eaten in W+, open diamonds = fat gain in W–. Calculated from data reported by Thompson *et al.* (1985).

growth, W+ sheep being less efficient than W– (Herd *et al*. 1993). Close examination of the response in body composition to feed intake indicates that post weaning rate of gain of lean per unit feed intake is greater in lines selected for high compared to low weaning weight (Figure 1; adapted from data of Thompson *et al*. 1985). These observations are consistent with differences in partitioning of feed energy and nitrogen intake between body and wool in pre–ruminant lambs from the same selection lines (Table 1, Oddy *et al*. 1989). In milk fed lambs, relationships between feed intake and weight gain, and between nitrogen intake and nitrogen retention in the whole body (including wool), do not differ between selection lines but partitioning of nitrogen (protein) between components of the body does differ. Weight plus lambs retain a higher proportion of N intake in their body than do W– lambs.

At the whole body level these results are consistent with observations of animals from other species where breeds of markedly different phenotype have been compared. Large White x Landrace and Meisham pigs apparently do not differ in the partial efficiency of nitrogen utilisation (Kyriazakis and Emmans 1995). However, our observations of sheep indicate that partitioning of protein deposition between organs (protein pools) occurs as a consequence of the phenotypic (single character) selection method used to generate genetically distinct lines of animals. This is perhaps not surprising in a species such as sheep in which significant quantities of protein are retained external to the body as wool.

How has genetic selection altered the response of lean body tissue to nutrient intake? Our major focus has been the response to feed intake of protein synthesis and degradation in muscle. We have shown that the response of protein synthesis and degradation in hind limb muscle to feed intake is different between lines of sheep selected for and against weight gain. Moreover, the rate of energy utilisation (oxygen uptake) by muscle differs between lines; W– lambs have higher rates of oxygen consumption per kg of hind–limb muscle (Oddy *et al*. 1995) (Table 2). Accordingly the energy cost of maintaining and growing muscle is higher in W– than W+ lambs. In sheep selected for weight gain the response to increased feed intake includes a decreased rate of protein degradation and diminished increment in rate of protein synthesis compared to animals selected for low rate of weight gain. Apart from variation in partitioning of retained nitrogen between body and wool, and protein degradation in muscle there are many other associated changes in response to selection for weight gain. These include: digestion of

Table 1 Retention of nitrogen in the body of pre–ruminant lambs from lines selected for (W+) and against (W–) weaning weight (R = randomly selected control line). Lambs were allowed *ad libitum* access to milk replacer. Data are means for the period from 40 to 80 d of age (from Oddy *et al.* 1989).

	Genotype			
	W+ n = 11	**R n = 10**	**W– n = 11**	**Difference**
Intake (g DM/d)+	340	263	192	*
Live weight gain (g/d)	240	171	132	*
N retention (g/d)	6.6	5.7	5.0	*
Body protein gain (g/d)	32	21	16	*
Body fat gain (g/d)	17	23	17	NS
N retained in body++	0.82	0.62	0.50	*

+ The diet contained 24.1 MJ and 265 g crude protein /kg dry matter (DM)
++Ratio of body N gain/N retention calculated from N balance
* Difference between selection lines P<0.05

Table 2 Relationships between feed intake (I, g/kg liveweight/d) and hind limb muscle protein syntheses and degradation (nmoles phenylalanine/kg hind limb/min) in castrate male lambs from lines selected for (W+) and against (–) weaning weight. Also shown is oxygen uptake (μmoles/kg hind limb/min) (from Oddy *et al.* 1995).

	Genotype			
	W+		**W–**	
Protein synthesis	$209+53.4*I-1.64*I^2$	(P<0.05)	380 + 21.4*I	NS
Protein degradation†	858–16.2*I	(P<0.01)	515 + 12.2*I	NS
Oxygen uptake†	88 ± 5.2		125 ± 9.5	

†Difference between selection lines P<0.05

feed, high growth lines digesting the same feed to a greater extent (Herd *et al*. 1993); plasma IGF = 1 concentration is higher in high growth lines (Speck *et al*.1989); responsiveness of plasma insulin concentration to feed intake is greater in high growth lines (Speck 1994); responsiveness of hind limb (muscle) protein synthesis and degradation to insulin, high growth line animals being more responsive than low growth line animals (Oddy 1993; Oddy *et al*. 1995). Selection of Angus cattle on the basis of single character selection for yearling weight (Parnell *et al*. 1994) is associated with corresponding changes in response of hind limb muscle protein synthesis and degradation and oxygen uptake to feed intake (Oddy *et al*. 1998) (Table 3).

Changes in efficiency of conversion of feed to gain and in the rate of protein degradation in response to selection for growth and leanness have been observed in many species ranging from chickens (Pym 1990; Tomas *et al*. 1991) to rainbow trout (McCarthy *et al*. 1994). The most informative comparisons have been in chickens. Chickens from lines selected for lean gain, or increased efficiency of conversion of feed to gain, have lower rates of fractional protein breakdown than control line chickens (Pym 1990). Moreover, differences in fractional breakdown rate of protein are associated with differences in net efficiency of protein utilisation, such that decreased rates of fractional protein breakdown give rise to improved efficiency of protein gain (Tomas *et al*. 1991).

The above pattern of responses of muscle protein metabolism to feed intake is not universally observed in farm animals. For example, Harris *et al*. (1992) reported that in castrate male Suffolk sheep both protein synthesis and degradation increased in response to feed intake. Lobley (1998) reported briefly on differences in whole body protein degradation in diverse breeds of cattle, and showed some evidence of difference in response of protein degradation to feed intake.

It is important to draw a clear distinction about the inferences that can be drawn between experiments in which animals of different breeds are compared (sometimes across experiments and methodologies), and those which use animals of the same breed, but arising from lines selected for a particular trait over a number of generations. One weakness of many such comparisons is that animals are not compared at the same stage of maturity, nor from a common nutritional history. In the absence of other data on mature size for the lines of animals used, it is preferable to compare animals at the same age rather than at the same weight. A second consideration relates to the nature of genetic change in lines selected for a single trait compared to that between breeds. It could be expected that the genetic changes which lead to development of different breeds would be more complex than those resulting from direct selection for a trait within a breed. It could be anticipated that the latter would lead to a simpler, more directed change in the genome, albeit arising from the action of many genes.

The subcellular mechanisms by which genetic selection has brought about differences in response of protein degradation to feed intake are not yet elucidated. In sheep (McDonagh *et al*. 1999) and beef cattle (McDonagh 1998) we have observed associations between rate of protein degradation in muscle and activity of the calcium activated (calpain) protease (e.c. 3.4.22.17) system. In particular the calpain inhibitor calpastatin differs in Angus cattle selected for and against weight at one year of age. Cattle from lines selected for high growth rate to one year of age have higher calpastatin activity (and slower rates of myofibre fragmentation post–mortem) than cattle from lines selected for low growth rate. These observations are consistent with cytoskeleton rearrangements, and in muscle a myofibrillar disassembly acting as at least one of the rate limiting steps (Table 4; McDonagh *et al*. 1999).

The apparent discrepancy between variation in protein kinetics and oxygen consumption in skeletal muscle in response to feed intake, and apparent lack of agreement about variation in partial efficiency of nutrient deposition in the whole body is highlighted by the above discussion. It seems paradoxical that at least at the level

Table 3 Effect of selection for yearling weight in cattle on protein dynamics (nmole phenylalanine/kg hind limb/min) and oxygen uptake (μmole oxygen/kg hind limb/min) in hind limb muscle. Animals were yearling steers from lines selected for high and low growth ate to one year of age. They were fed the same diet at approximately maintenance or 1.6 x maintenance (data from Oddy *et al.* 1998).

	Genotype			
	High Diet		**Low Diet**	
	M	**1.6M**	**M**	**1.6M**
Protein synthesis	238 ± 45	215 ± 39	246 ± 45	425 ± 39*
Protein degradation	292 ± 100	196 ± 87	319 ± 100	332 ± 87
Oxygen uptake	118 ± 49	113 ± 42	100 ± 49	142 ± 42

*Selection line x nutrition interaction P<0.05

of a major tissue such as muscle there is variation in protein metabolism and energy utilising processes between individuals from selected populations, which should result in variation in partial efficiency of energy cost of protein deposition, yet at the whole body level such variation seems to be absent. One suspects the apparent disparity is merely an artifact of nutritional experiments using groups rather than individual animals as the experimental unit. From our experience in development of an understanding of the consequences of selection for growth traits, it is clear there is variation between individual animals about the relationship between intake and gain of farm animals (Herd *et al*.1993). Recent evidence indicates that this variation is heritable and is transmitted to progeny, at least in mice (Hill *et al.* 1998; Nielsen *et al.* 1998; Hughes *et al*. 1998) and beef cattle (Herd *et al*. 1997). There have as yet been no studies conducted on the partial efficiency of gain in cattle selected for divergence in intake with respect to growth. Nonetheless, within first generation progeny, there is divergence in calpastatin activity in muscle and associated changes in rate of myofibre disassembly post mortem (McDonagh *et al*. 1999; McDonagh 1998), and changes in heat production calculated from metabolisable energy intake minus energy retention (Richardson *et al*. 1999).

Observations of the relationship between food intake and gain at the level of individual animals suggests that variation in either or both of maintenance or partial efficiency of protein gain could exist in cattle. Theoretical considerations and practical observation indicate that variation in protein degradation may contribute to practical variation in efficiency of feed use at the whole animal level.

Other implications of data from selection experiments

Selection experiments in farm animals can lead to surprising results. Single character selection for and against wool growth in Merino sheep has generated lines of sheep in which wool growth differs more than two–fold (Williams 1979). As with selection for weight gain, many concomitant changes have occurred. Of particular interest was the observation that animals selected for high wool growth had, at the same feed intake, an uptake of alpha amino nitrogen in portal blood 30% higher than animals selected for low wool growth (Lush *et al*. 1991, Figure 2). Digestion of feed does not differ between these lines of sheep, but microbial protein production per unit feed is higher in sheep from lines selected for high wool growth (Kahn 1996; Table 5).

These observations suggest that, in ruminants, genetic selection for a trait on the periphery of the host (wool growth) can influence the supply of nutrient to the host by altering the environment in the rumen to one in which the bacterial population is capable of producing more of a potentially limiting nutrient. The implications of this observation on our attempts to model quantitatively the nutrient supply to ruminants are clear. They indicate that models of nutrient supply should consider a genetic component not just on response at the host animal level but also in nutrient supply, both in total tract digestibility and in amino acid supply per unit feed digested.

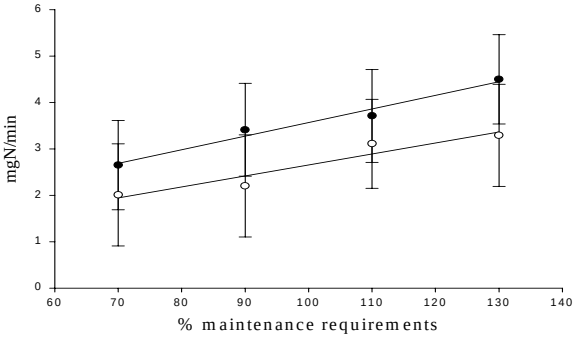

Figure 2 Uptake of α–amino nitrogen into portal blood of sheep selected for (solid circles ± s.e.) and against (empty circles) wool growth at different rates of feed intake (data from Lush *et al.* (1991).

Table 4 Calpain system activity in *M. longissimus dorsi* of Angus Cattle selected for (high) or against (low) growth to one year of age or not selected (control) (from McDonagh 1998).

	Genotype		
	High n = 10	**Control n = 10**	**Low n = 10**
Calpastatin	3.60±0.11	3.50±0.12	3.16±0.12*
μ–Calpain	2.02±0.12	2.05±0.13	2.22±0.13
m–Calpain	2.95±0.08	2.90±0.08	2.81±0.08

*Difference between selection lines P<0.05

Effects of mutations in a single gene

Occasionally single gene effects of practical value become fixed in populations, giving rise to breeds of animals with markedly different phenotypes. One example is the double muscled breeds of European cattle (e.g. Belgian Blue, Peidmontese). Grobet *et al*. (1997) and Kambadur *et al*. (1997) showed that double muscling resulted from a mutation in the gene for myostatin, a member of the TGFb1 superfamily (Georges *et al*. 1998). The double muscled phenotype is asssociated with either the homozygous or the compound heterozygous state at the *mh* locus on chromosome 2. In ten European cattle breeds, five myostatin mutations account for the double muscled phenotype. Enlargement of muscles is due primarily to hyperplasia of muscle fibres and this phenotype can be observed during foetal life (Arthur 1996), as can biochemical phenotypes (Gagniere *et al*. 1997). An increase in the proportion of type IIb fibres and a lower density of capillaries in muscles of production interest also occurs in double muscled animals (Stavaux *et al*. 1993). The amount of connective tissue present in muscles of double muscled cattle is not commensurately increased by the *mh* mutation (Arthur 1996), presumably because myostatin expression is of little functional significance to fibroblasts.

Another potentially useful single gene effect is the callipyge mutation in sheep (Cockett *et al*.1996; Freking *et al*. 1998). The callipyge mutation is associated with enhanced skeletal muscle growth, which becomes perceptable at 4–6 weeks post–partum. Mass of selected hind–limb muscles (e.g. *M. biceps femoris*) may increase to >40% compared to the same muscle in control lambs at 6 months post–partum (Koohmaraie *et al*. 1995). Unlike the mutation at the *mh* (cattle, double muscle) locus, the callipyge mutation seems to result more in hypertrophy of fast oxidative and fast glycolytic fibres in muscle, rather than an increase in number (hyperplasia) of muscle fibres (Carpenter *et al*. 1996). Recent data (Lorenzen *et al*. 1999) indicate that affected muscles in callipyge lambs increase protein accretion through a concomitant reduction in protein degradation and synthesis. There is not yet evidence of changes in transcriptional and translational efficiency. Increased calpastatin activity has been observed in association with callipyge muscle hypertrophy (Lorenzen *et al*. 1999).

One of the more important observations in the callipyge genotype is that muscle protein mass is increased at the 'expense' of some internal organs; in particular, liver weight is reduced in callipyge lambs (Lorenzen *et al*. 1999). Variation in partitioning of protein accretion (and metabolism) between organs is consistent with observations on weight and fleece selection lines of sheep that protein accretion is redistributed between body gain and wool. Such genetic changes would be expected to alter the efficiency of utilisation of energy for protein accretion in the whole body, even if efficiency at the organ level were considered constant, which the above evidence indicates is unlikely.

Conclusions

The information reviewed suggests that partial efficiency of protein gain, at least in muscle, exhibits genetic variation. Given that selection for production traits can lead to partitioning of protein to different body organs, then it is plausible that variation in partial efficiency of protein gain in the whole body should exist. I believe failure to conclusively demonstrate such variation reflects more on our experimental methodology than on reality. The challenge for the future is to develop tools for repeated measures in individual animals of traits which affect efficiency of nutrient use. If it indeed can be demonstrated that genetic variation in partial efficiency exists, then the structure of present feeding systems will require serious revision.

Table 5 Weight, fleece production, digestible dry matter intake and yield of microbial nitrogen from the rumen of ewes selected for (Fleece Plus) and against (Fleece Minus) clean fleece weight. Microbial nitrogen (MN) excretion was calculated from urinary excretion of purine derivatives. Values are mean ± s.e. (from Kahn 1996).

	Genotype		
	Fleece plus	**Fleece minus**	
Fleece free live weight (kg)	39.5 ± 1.06	43.0 ± 1.14	*
Annual Fleece Weight (kg)	5.6 ± 0.17	1.9 ± 0.15	**
Intake of Digestible dry matter (g/$W^{0.75}$/d)	25.1 ± 0.86	21.6 ± 0.92	*
Microbial – N (MN, g/d)	8.9 ± 0.45	7.0 ± 0.47	**
MN/DMI (g/kg)	11.2 ± 0.29	10.3 ± 0.31	*
MN/N intake (g/g)	0.61 ± 0.020	0.55 ± 0.021	*

*Selection lines differ P<0.05, ** P<0.01

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References

Arthur, P. F. (1996). Double muscling in cattle: a review. *Australian Journal of Agricultural Research* **46**, 1493–515.

Bunger, L., MacLeod, M.G., Wallace, C.A. and Hill, W.G. (1998). Direct and correlated effects of selection for food intake corrected for body weight in the adult mouse. *Proceedings of the 6th World Congress of Genetics Applied to Livestock Production* **26,** 97–100.

Carpenter, C.E., Rice, Q.D., Cockett, N.E. and Snowder, G.D. (1996). Histology and composition of muscles from normal and callipyge lambs. *Journal of Animal Science* **74,** 388–393.

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

Freking, B.A., Kelle, J.W., Beattie, C.W., Kappes, S.M., Smith, T.P.L., Sonstegard, T.S., Nielsen, M.K. and Leymaster, K.A. (1998). Evaluation of the ovine callipyge locus: I relative chromosomal position and gene action. *Journal of Animal Science* **76,** 2062–2071.

Gagniere, H., Picard, B., Jurie, C. and Geay, Y. (1996). Comparative study of metabolic differentiation of foetal muscle in normal and double–muscled cattle. *Meat Science* **45**, 145–52.

Georges, M., Grobet, L., Poncelet, D., Royo, L.J., Pirottin, D. and Brouwers, B. (1998). Positional candidate cloning of the bovine *mh* locus identifies an allelic series of mutations disrupting the myostatin function and causing double–muscling in cattle. *Proceedings of the 6th World Congress of Genetics Applied to Livestock Production* **26**, 195–204.

Harris, P.M., Skene, P.A., Buchan, V., Milne, E., Calder, A.G., Anderson, S.E., Connell, A. and Lobley, G.E. (1992). Effect of food intake on hind–limb and whole–body protein metabolism in young growing sheep:chronic studies based on arterio–venous techniques. *British Journal of Nutrition* **68,** 389–407.

Herd, R.M., Archer, J.A., Arthur. P.F., Richardson, E.C., Wright, J.H., Dibley, K.C.P. and Burton, D.A. (1997). *Proceedings of the Association for the Advancement of Breeding and Animal Genetics* **12,** 742–745.

Herd, R.M., Oddy,V.H. and Lee, G.J. (1993). Effect of divergent selection for weaning weight on liveweight and wool growth responses to feed intake in Merino ewes. *Australian Journal of Experimental Agriculture* **33,** 699–705.

Hughes, T.E., Archer, J.A. and Pitchford, W.S. (1998). Response to selection for high and low net feed intake in mice. *Proceedings of the 6th World Congress of Genetics Applied to Livestock Production* **25,**105–108.

Kahn, L.P. (1996). Differences between Merino selection lines in microbial yield from the rumen and utilisation of protein for wool growth. PhD Thesis, University of New England.

Kambadur, R., Sharma, M., Smith, T. P. L., and Bass, J. J. (1997). Mutations in myostatin (GDF8) in Double–muscled Belgian Blue and Piedmontese cattle. *Genome Research* **7,** 910–6.

Koohmaraie, M., Shackleford, S.D., Wheeler, T.L, Lonergan, S.M. and Doumit, M.E. (1995). A muscle hypertrophy condition in lamb (callipyge): characterisation of effects on muscle growth and meat quality traits. *Journal of Animal Science* **73,** 3596–3607.

Kyriazakis, I. and Emmans, G. (1995). Do breeds of pig differ in the efficiency with which they use a limiting protein supply? *British Journal of Nutrition* **74,** 183–195.

Lobley, G.E. (1998). Nutritional and hormonal control of muscle and peripheral tissue metabolism in farm species. *Livestock Production Science* **56,** 91–114.

Lorenzen, C.L., Koohmaraie, M., Shackelford, S.D., Jahoor, F., Freetly, H.C., Wheeler, T.L., Savell, J.W. and Fiorotto, M.L. (1999). Protein kinetics in callipyge lambs. *Journal of Animal Science* (in press).

Lush, J.M., Gooden, J.M. and Annison, E.F. (1991). The uptake of nitrogenous compounds from the gut of sheep genetically different in wool production. *Proceedings of the Nutrition Society of Australia* **16,** 144.

McCarthy, I.D., Houlihan, D.F. and Carter, C.G. (1994). Individual variation in protein turnover and growth efficiency in rainbow trout, Oncorhynchus mykiss (Walbaum). *Proceedings of the Royal Society London* **B 257,** 141–147.

McDonagh, M.B. (1998). Calpain activity affects muscle protein turnover and meat tenderisation. PhD Thesis, University of New England.

McDonagh, M.B., Fernandez, C. and Oddy, V.H. (1999). Hind=limb protein metabolism and calpain system activity influence post–mortem changes in meat quality of lamb. *Meat Science* **52,** 9–18.

Nielsen, M.K. (1998). Genetic variation in feed energy utilisation in mice. *Proceedings of the 6th World Congress of Genetics Applied to Livestock Production* **26,** 89–96.

Oddy, V.H., (1993). Regulation of muscle protein metabolism in sheep and lambs: nutritional, endocrine and genetic aspects. *Australian Journal of Agricultural Research* **44,** 901–913.

Oddy, V.H., Herd, R.M., McDonagh, M.B., Woodgate, R., Quinn, C.A. and Zirkler, K. (1998). Effect of divergent selection for yearling growth rate on protein metabolism in hind=limb muscle and whole body of Angus cattle. *Livestock Production Science* **56,** 225–231.

Oddy, V.H., Speck, P.A., Warren, H.M. and Wynn, P.C. (1995). Protein metabolism in lambs from lines divergently selected for weaning weight. *Journal of Agricultural Science, Cambridge* **124,** 129–137.

Oddy, V.H., Warren, H.M., Ewoldt, C.L. and Riley, K.D. (1989). Pre=weaning growth and body composition of lambs genetically different in weaning weights. *Proceedings of the Nutrition Society of Australia* **14,** 139.

Parnell, P.F., Herd, R.M., Perry, D. and Bootle B. (1994). The Trangie experiment—responses in growth rate, size, maternal ability, reproductive performance, carcass composition, feed requirements and herd profitability. *Proceedings of the Australian Society of Animal Production* **20,** 17–20.

Pattie, W.A. and Williams, A.J. (1966). Growth and efficiency of post weaning gain in lambs from Merino flocks selected for high and low weaning weight. *Proceedings of the Australian Society of Animal Production* **6,** 305–309.

Pattie, W.A. and Williams, A.J. (1967). Selection for weaning weight in Merino sheep 3. Maintenance requirements and the efficiency of conversion of feed to wool in mature ewes. *Australian Journal of Experimental Agriculture and Animal Husbandry* **7,** 117–125.

Pym, R.A.E. (1990). Nutritional genetics. In: *Poultry Breeding and Genetics,* pp. 847–876 (ed. R.D. Crawford). Elsevier, Amsterdam.

Richardson, E.C., Herd, R.M., Oddy, V.H., Woodgate, R.T., Archer, J.A. and Arthur, P.F. (1999). Body composition explains only part of the intake difference between high and low efficiency Angus steers. *Recent Advances in Animal Nutrition in Australia* **12,** 4A.

Speck, P.A., Oddy, V.H. and Wynn, P.C. (1989). Insulin—a role in regulation of growth potential. *Proceedings of the Nutrition Society of Australia* **14,** 108.

Speck. P.A. (1991). Metabolic hormones as indicators of growth potential in sheep. PhD Thesis, University of New England.

Speck, P.A. and Morris, C.A. (1996) .Selection for yearling weight in Angus cattle: Impact on the calpain system and meat tenderness. *Journal of Animal Science* **74** (Suppl 1), 157.

Stavaux, D., Art, T., McEntee, K., Reznick, M. and Lekeux, P. (1993). Muscle fibre type and size, and muscle capillary density in young double–muscled Blue Belgian cattle. *Zentralblatt fuer Veterinaermedizin Reihe A* **41**, 229–36.

Thompson, J.M. Parks, J.R. and Perry, D. (1985). Food intake, growth and body composition in Australian Merino sheep selected for high and low weaning weight. *Animal Production* **40,** 55–70.

Tomas, F.M., Pym, R.A.E. and Johnson, R.J. (1991). Muscle protein turnover in chickens selected for increased growth rate, food consumption or efficiency of food utilisation: Effects of genotype and relationship to plasma IGF–1 and growth hormone. *British Poultry Science* **32,** 363–376.

Williams, A.J. (1979). Speculation on the biological mechanisms responsible for genetic variation in the rate of wool growth. In: *Physiological and Environmental Limitations to Wool Growth,* pp. 337–354 (eds. J.L. Black and P.J. Reis). University of New England Press.