2007

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Animal (2007), **1:10**, pp 1427–1434 © The Animal Consortium 2007
doi: 10.1017/S1751731107000808

Genetic selection, sex and feeding treatment affect the whole-body chemical composition of sheep

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(Received 9 January 2007; Accepted 22 August 2007)

Hypotheses on total body chemical composition were tested using data from 350 Suffolk sheep grown to a wide range of live weights, and fed in a non-limiting way, or with reduced amounts of feed, or ad libitum *on feeds of reduced protein content. The sheep were from an experiment where selection used an index designed to increase the lean deposition rate while restricting the fat deposition rate. Ultrasound muscle and fat depths were the only composition measurements in the index. The animals were males and females from a selection (S) line and its unselected control (C). The protein content of the lipid-free dry matter was unaffected by live weight, sex or feeding treatment with only a very small effect of genetic line (0.762 kg/kg in S and 0.753 kg/kg in C;* $P < 0.05$*). The form of the relationship between water and protein was not affected by any of the factors; in the different kinds of sheep it was consistent with no effect other than through differences in mature protein weight. The water : protein ratio at maturity was estimated as 3.45. Over the whole dataset, lipid weight (*L*) increased with protein weight (*P*) according to* $L = 0.3135 \times P^{1.850}$*. Allowing for this scaling, fatness increased on low-protein feeds, was greater in females than in males and in C than in S (*$P < 0.001$*). Lipid content (g/kg fleece-free empty body weight) was reduced by restricted feeding only in males at the highest slaughter weight (114 kg). The lines differed in lipid content (*$P < 0.001$*) with means of 265.1 g/kg for C and 237.3 g/kg for S. Importantly, there was no interaction between line and feeding treatments. A higher proportion of total body protein was in the carcass in S than in C (0.627* v. *0.610;* $P < 0.001$*). For lipid, the difference was reversed (0.736* v. *0.744;* $P < 0.05$*). The total energy content increased quadratically with slaughter weight. At a particular weight, the energy content of gain was higher in females than in males and in C than in S. Genetic selection affected body composition at a weight favouring the distribution of protein to the carcass and lipid to the non-carcass. Once allowing for effects of genetic selection, sex and feeding treatment on fatness, simple rules can be used to generate the chemical composition of sheep.*

Keywords: carcass composition, fatness, feeding treatment, genetic selection, sheep

Introduction

The main changes in the chemical composition of domestic animals as they grow were outlined by Armsby and Moulton (1925). These are that fatness increases, the water content of the fat-free body decreases and the protein content of the lipid-free dry matter changes little. These effects are well illustrated for sheep by the data of Blaxter *et al.* (1982) and Jenkins and Leymaster (1993). Emmans (1988) suggested how these changes could be qualitatively and quantitatively described. However, within the general trends, it is possible that there are systematic effects of different genotypes, including those brought about by artificial selection, sex and feeding treatment that need to be accounted for in animal growth modelling.

An approach to modelling the growth (Black *et al.*, 1986; Emmans, 1988; Whittemore, 1993) is to build up the chemical body from body protein using the steps outlined in Figure 1. Protein weight is used to predict lipid-free dry weight as well as water weight. Lipid is then predicted from protein weight together with the supply of energy and nutrients. In addition, such prediction of chemical growth is necessary to calculate nutrient requirements (National Research Council, NRC, 1985; Agricultural and Food Research Council (AFRC), 1993).

The data in this study were from both sexes of Suffolk sheep of different genetic lines fed in different ways and

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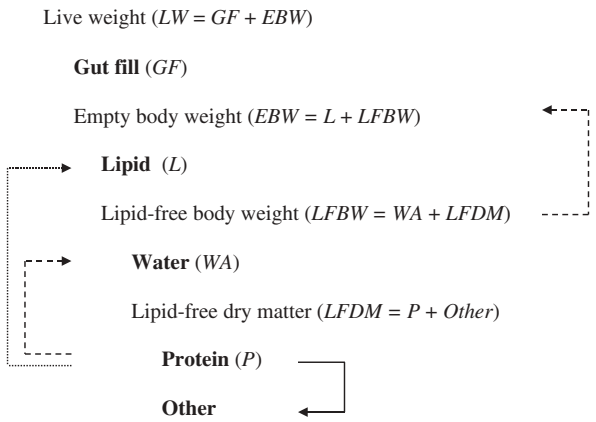

Figure 1 Schematic of analytical approach adopted. The primary quantities are shown in bold. Close to constant relationships are shown as solid lines, relationships that may be affected by genotype and environment are shown as dashed lines, and that which is certainly affected by genotype and environment is shown as a dotted line.

slaughtered over a wide range of weights. The following hypotheses were tested: (i) the protein content of the lipid-free dry matter would be unaffected by live weight, genetic line, sex or feeding treatments; (ii) water weight (*WA*) would be an exponential function of protein weight (*P*), $WA = a \times P^b$; (iii) the value of the exponent, *b*, would not be affected by genetic line or sex; (iv) the value of the scalar, *a*, would not be affected by feeding treatment but would increase with mature protein weight; (v) the relationship between lipid and protein weights would be affected by genetic line, sex and feeding treatment; and (vi) the energy content of the chemical body would be a quadratic function of slaughter weight with the coefficients affected by genetic line and sex.

Material and methods

The animals that provide the data considered here, and their treatments, have been fully described by Lewis *et al.* (2002b and 2004). Briefly, rams born in the 9th year of selection in the Scottish Agricultural College (SAC) Suffolk selection experiment were used to produce the purebred lambs used in these studies. The lambs were born in 1994, 1995 and 1996. Selection had been based on an index designed to increase the rate of lean deposition while restricting the rate of fat deposition (Simm and Dingwall, 1989; Simm *et al.*, 2002). The traits combined in the selection index were live weight, and ultrasonic muscle and fat depths measured at the 13th rib and 3rd lumbar vertebrae. Lambs from both the selection (S) line and from its unselected control (C) were used.

Experimental design

The Animal Experiment Committee at SAC approved all procedures and protocols used in the experiment.

Table 1 *Composition of the feeds*

	Feed		
	H	M_P	L_P
Ingredient (g/kg)			
Barley	582.5	504.2	464.0
Dried grass	200.0	66.7	0.0
Oatfeed	0.0	31.0	46.7
Citrus pulp	0.0	233.0	350.0
Hipro soya-bean meal	70.0	34.4	16.7
Fish meal	60.0	20.0	0.0
Molasses	50.0	63.0	70.0
Protected fat	0.0	11.0	16.6
Mineral and vitamin mix	37.5	36.7	36.0
Chemical composition†			
DM (g/kg)	880	882	878
CP (g/kg DM)	192	141	120
NDF (g/kg DM)	242	228	212
AHEE (g/kg DM)	26	30	28
Ash (g/kg DM)	87	81	73
NCGD (g/kg DM)	789	826	845
ME (MJ/kg DM)‡	11.7	12.3	12.5

†Abbreviations are: H – high protein; M_P – medium protein; L_P – low protein; DM – dry matter, CP – crude protein, AHEE – acid-hydrolysed ether extract, NCGD – neutral cellulase gamanase digestibility, ME – metabolisable energy.
‡Predicted from 0.014 NCGD + 0.025 AHEE (Thomas *et al.*, 1988).

The experiment was designed mainly to investigate how carcass composition was affected by genetic line. To investigate the possible interactions, measurements were made over a wide range of live weight on animals given different nutritional treatments. Both sexes were used. The opportunity was taken to chemically analyse both the carcass and non-carcass (all of the shorn empty body, except for the carcass and the blood) components of a subsample of the animals dissected for carcass evaluation.

There were five target slaughter points that coincided with live weights: near birth (SP1), at weaning (SP2), at an intermediary point (SP3), at selection (SP4) and nearing maturity (SP5). The weights at SP4 were chosen to approximate those at the selection age of 150 days in the flock at the conclusion of a performance testing regime. The weights at any one slaughter point were 1.73 times those at the preceding slaughter point, corresponding to equidistant steps on a logarithmic scale.

There were two feeding experiments. The first (Lewis *et al.*, 2002b), in 1995, used three levels of feeding: high (H), medium (M_f) and low (L_f). Treatment H involved *ad libitum* access to a non-limiting feed (feed H; Table 1). Treatment L_f was designed to give about half the growth rate of H, with treatment M_f intermediate. The second (Lewis *et al.*, 2004), in 1996, used three levels of dietary protein (Table 1) offered *ad libitum*: high (H), medium (M_p) and low (L_p). The feeds L_p and M_p were designed to give growth rates comparable with L_f and M_f, respectively. The lowest growth rate was intended to be similar to that seen in commercial

Table 2 *Design for the 1995 and 1996 experiments showing target live weights (LW) for the three slaughter points (SP) used. The numbers were repeated for selection and control line animals.*

	Male				Female				
	Feed†				Feed†				
SP	H	M	L	LW	H	M	L	LW	*n*
SP3	5	5	5	38.1	5	5	0	33.1	25
SP4	5	5	5	66.0	5	5	0	57.5	25
SP5	5	5	0	114.0	5	5	0	100.0	20
n	15	15	10		15	15	0		70

†Three general categories of feed were used: high (H), medium (M) and low (L).

systems. Prior to the start of the feeding treatments at SP2 all lambs were offered feed H.

In each experiment, the design shown in Table 2 was used. In total 280 animals were slaughtered at SP3, SP4 and SP5. Data from an additional 70 animals were also used. Of these, 40 were killed at SP1; half were males and half were females from each of the two lines, evenly distributed between 1995 and 1996. In females and males, weights at SP1 were 10.9 and 12.7 kg, respectively. From 1994, data from five selection line males at SP2 at a weight of 22.0 kg, 10 selection line males fed *ad libitum* on feed H with half at each of SP4 and SP5, and 15 selection line females at SP4 with one-third on each of feed H, L_p and L_f were also used. In total, the experiments involved 350 animals.

Slaughter procedure

Except for SP1, animals were shorn the day before slaughter. On the day of slaughter, the animals were weighed and transported to the SAC Carcass Evaluation Unit. The animals were stunned with a captive bolt, the jugular vein cut and the blood collected and weighed. The gastro-intestinal tract was weighed before and after emptying, and the weights of the other non-carcass components recorded. All of the non-carcass components, excluding only the blood, were frozen and stored. The carcass was weighed before and after chilling overnight, and then split, shrouded, frozen and stored.

Analytical methods

After partial defrosting, the right side of each carcass and the non-carcass components were weighed, thoroughly minced to be homogeneous and duplicate samples of each taken for chemical analyses (dry matter (DM) and the nitrogen (N), ash and gross energy (GE) contents of the DM). The DM was determined by freeze-drying to constant weight. The DM was analysed for protein (6.25 N) by a micro-Kjeldhal procedure, and for ash by burning in a muffle furnace at 550°C. The GE of the DM was determined by adiabatic bomb calorimetry.

Lipid content was calculated from the GE and N values using the equation of Kyriazakis and Emmans (1992):

$$\text{lipid}\,(\text{g/g DM}) = (\text{GE}\,(\text{kJ/g DM}) - (23.8 \times 6.25\,\text{N}\,(\text{g/g DM})))/39.6, \quad (1)$$

which assumes that the energy contents of protein and lipid are 23.8 and 39.6 kJ/g, respectively. Lipid content was calculated in this way because it had been shown (Kyriazakis and Emmans, 1992) that the sum of the measured lipid, protein and ash contents in the DM showed systematic deviations from unity due to treatment. The deviations with the lipid content calculated from equation (1) did not show such systematic effects. With the lipid content calculated from N and GE contents, and the protein content calculated as 6.25 N, there is an inevitable formal dependency between our values for lipid and protein contents. Across both carcass and non-carcass samples, the GE and 6.25 N values were very highly correlated ($r = -0.969$). However, as the DM is necessarily a mixture of 6.25 N (protein), ash, which exists in virtually constant ratio to protein, and lipid, which is proportional to the GE not coming from protein, such is always the case irrespective of how its components are determined. The chemical components of the blood were added to the carcass and non-carcass to produce the chemical empty body.

Statistical methods

The variables analysed were as follows: (i) protein content of the lipid-free dry matter; (ii) water weight in relation to protein weight; (iii) lipid weight in relation to protein weight; (iv) lipid content of the fleece-free empty body; (v) the proportions of total body, total protein and total lipid that were in the carcass; and (vi) the total energy content of the chemical body.

ANOVA. The overall effects of SP, genetic line, sex and feeding treatment on composition variables were investigated by developing consistent subsets of data suitable for ANOVA. Four different factorial analyses were used. The first and second analyses both used 120 animals. The full factorial arrangement for both was three slaughter points (SP3, SP4 or SP5), two genetic lines (S or C), two sexes (male or female) and two feeding treatments (H or M). There were five animals per treatment combination, as shown in Table 2. In the first analysis, M was M_f (Lewis *et al.*, 2002b) and in the second M_p (Lewis *et al.*, 2004). The third and fourth analyses both used 60 male animals. The full factorial arrangement for both was two slaughter points (SP3 or SP4), two genetic lines (S or C) and three feeding treatments (H, M or L). There were five animals per treatment combination, as shown in Table 2. For the third analysis, M and *L* were M_f and L_f, respectively (Lewis *et al.*, 2002b), and for the fourth M_p and L_p, respectively

(Lewis *et al.*, 2004). The general structure of the model fitted was

$$y_{ijkl} = \mu + G_i + T_j + R_k + (GT)_{ij} + (GR)_{ik} + (TR)_{jk} + (GTR)_{ijk} + \varepsilon_{ijkl},$$

where y was the response variable for a lamb from Suffolk line G, on feeding treatment T and of sex R. The two (GT), (GR), (TR)) and three-way (GTR) interactions among these factors, along with residual error (ε), were also included in the model. For the first and second analyses, all effects were present. For the third and fourth analyses, the term for sex and its interactions were excluded as only males were used.

As noted earlier, data were available for some combinations of treatment factors in the 1994 experiments, and at SP1 in the 1995 and 1996 experiments. Including them caused imbalance in the factorial design. Alternative approaches for analysing such imbalanced data, such as Residual Maximum Likelihood, proved inappropriate since certain treatment combinations were exclusive to the 1994 experiment. As a solution, two-way ANOVA was used defining one main effect as the different combinations of treatment factors, such as feeding treatment/sex/SP, across which the other main effect, such as genetic line, could be compared. The combination of factors is henceforth referred to as 'case'.

Regression analyses. Regression was used to explore the relationship between: (i) water and protein weights; (ii) lipid and protein weights; (iii) the proportions of the total body, total protein and total lipid that were in the carcass, and body weight; and (iv) total body energy content and chemical body weight. Regression models of the form $Y_i = a \times X_i^b$ were fitted for (i) and (ii) above, and index values (I_i) for individuals were calculated as Y_i/X_i^b, which were then treated as a variable. For (iii), a polynomial of order three was fitted for descriptive purposes. For (iv), a quadratic form was used.

We could not assume *a priori* that there would be no effects of feeding treatment on the weight of water at a protein weight. Were there such effects, the estimate of the value of the exponent using all of the data could be biased as some feeding treatments (L_f and L_p) were not represented at SP5. To avoid this possible problem, a subset of data from the animals fed H *ad libitum* was used to test for possible effects of line and sex on the value of the exponent, b.

On the assumption that the relationship between water weight (WA, kg) and protein weight (P; kg) can be described as the exponential function $WA = a \times P^b$ then, if b has the same value for all genotypes, it follows that $WA_m = a \times P_m^b$, where m represents the mature values of the two variables. If, in addition, the value of b is not unity, then the value of a must differ across genotypes. Furthermore, it follows that $a = WA_m/P_m^b$. For genotypes with different values of P_m, but with the same water : protein ratio at a maturity of $k = WA_m/P_m$, it must be the case that $a = k \times P_m^{(1-b)}$. Where values of a can be estimated from data and combined with prior estimates of P_m for different genotypes, the hypothesis that k is essentially constant can be evaluated. Estimates of P_m were taken from: (i) the estimates of mature weight for the males and females of the S and C lines (Lewis *et al.*, 2006); and (ii) the estimates of protein weight at these weights from the logarithmic regressions of protein weight on slaughter weight.

For some purposes, the variables were log transformed. This equalized variances across the range of the data and made relationships between variables more nearly linear. An added advantage of using the log transformation is that the residual standard deviation (r.s.d.) of a regression equation is a proportional measure, and thereby reflects the extent of measurement error for individual observations.

There were differences between slaughter points in the average length of time that the carcasses were stored. Using the linear effect of storage time as a variable accounted for the apparent effects of slaughter point on the relationship between water and protein, and this was fitted as a variable in the regression of water on protein.

There was a strong curvilinear effect of chemical body weight on the proportions of total body, total protein and total lipid that were in the carcass ($P < 0.01$). Chemical body weight was therefore fitted (linear, quadratic and cubic terms were included) as a covariate when looking at the effects of the treatments by ANOVA.

In some systems for calculating energy requirements (NRC, 1985; AFRC, 1993), the energy per unit gain in weight needs to be known. In order to allow our data to be seen in this way, total content of energy in the chemical body (TEC; MJ per animal) was related to slaughter weight (SW; kg per animal) for both sexes of the two lines that were fed *ad libitum* on H. Parks (1982) produced evidence that the energy content per unit weight of the animal increased linearly with its weight so that $TEC/SW = a + (b \times SW)$, at least in some circumstances. It follows that $TEC = (a \times SW) + (b \times SW^2)$. The energy content of the gain in weight can then be found by differentiation as $dTEC/dSW = a + (2 \times b \times SW)$.

All analyses were conducted using GenStat (2005).

Results

Protein content of the lipid-free dry matter

There were no significant effects of either feeding treatment or sex on the protein content of the lipid-free dry matter in the body. There was a very small difference between the lines (0.762 kg/kg in S and 0.753 kg/kg in C; s.e.d. 0.0027 kg/kg; $P < 0.05$). There were no systematic effects of slaughter point.

Water weight as a function of protein weight

Log water weights were regressed on log protein weights, and on storage time as a linear variable to allow for water loss during storage. The slope of the regression was 0.9182 (s.e. 0.00531; R^2 0.993; r.s.d. 0.0421), which is less than unity ($P < 0.001$). Water weight corrected to zero storage time is plotted against protein weight in Figure 2, on linear

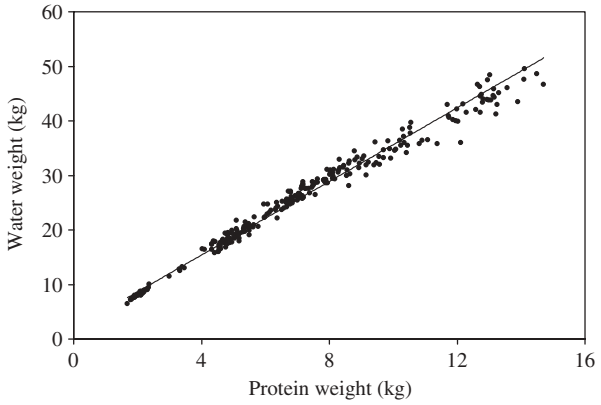

Figure 2 Relationship of body water (*WA*; kg), adjusted to zero storage time, on body protein (*P*; kg) for 350 sheep. The regression was $WA = 4.311 \times P^{0.9182}$ (R^2 0.993; r.s.d. 0.0421 of an observation).

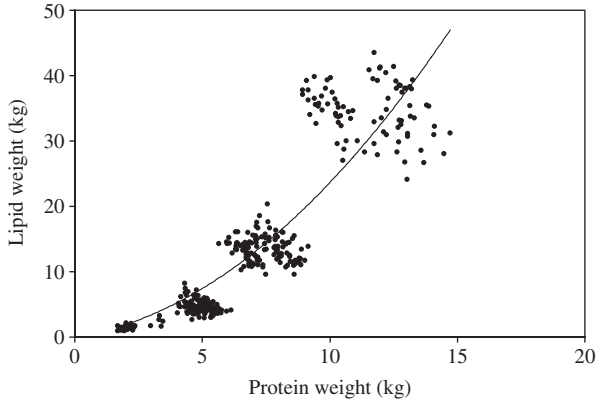

Figure 3 Relationship between body lipid (*L*; kg) and body protein (*P*; kg). The regression was $L = 0.3135 \times P^{1.850}$ (R^2 0.890; r.s.d. 0.347 of an observation).

scales; the increased absolute variation about the trend line can be seen.

When the data were restricted to those animals on feed H fed *ad libitum* ($n = 140$) the model fitted with a common slope was not significantly worse than where the line–sex combinations were allowed different values ($P > 0.15$). Using the common slope (0.9094; s.e. 0.00922; R^2 0.988; r.s.d. 0.0384), there were no significant effects of line or sex on the value of the intercept. However, the value was greater for males and for S.

The water index (calculated as body water/(body protein$^{0.9094}$)) was not affected by the level of feeding, with a mean of 4.39 (s.e. 0.012). The index increased to a slight extent ($P < 0.05$) as the protein content of the feed used was reduced (4.41 (s.e. 0.023) for M_p; 4.48 (s.e. 0.036) for L_p).

Fatness

Lipid weight as a function of protein weight. Lipid weight is plotted against protein weight on linear scales in Figure 3. The variation at any weight was substantial. In general, the lipid-to-protein ratio increased as the animals grew. The absolute level of variation increased appreciably as protein

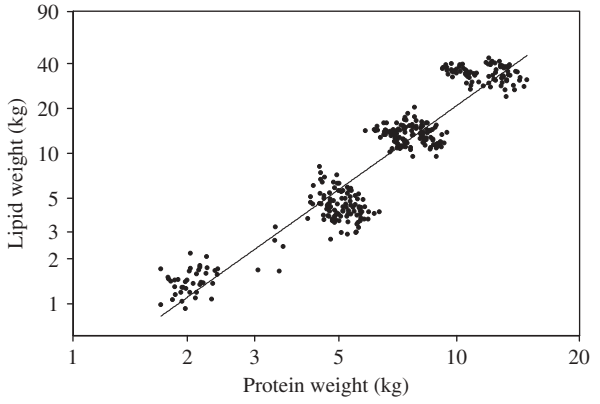

Figure 4 Linear regression of body lipid (*L*) weight (kg) on body protein (*P*) weight (kg) on log scales. The regression was $L = 0.3135 \times P^{1.850}$ (R^2 0.890; r.s.d. 0.347 of an observation). The axes on the plot are shown on the original scale.

Table 3 *Effects*[†] *of line, sex and feeding treatment on the lipid index*[‡]

Factor	Level	*n*	Lipid index
Line	Selection	190	0.3083
	Control	160	0.3732
	s.e.d.		0.0105
Sex	Male	195	0.2931
	Female	155	0.3884
	s.e.d.		0.0105
Feed[§]	H	140	0.3202
	M_f	60	0.3188
	L_f	25	0.3174
	M_p	60	0.3566
	L_p	25	0.4166
	Max s.e.d.		0.0266
	Min s.e.d.		0.0146

[†]Effects of line, sex and feed protein content were significant ($P < 0.001$); level of feeding was not significant ($P > 0.2$).
[‡]Lipid index = lipid weight (g)/[body protein weight (kg)]$^{1.850}$.
[§]Feeds H, M_p and L_p are described in Table 1 and were offered *ad libitum*; treatment L_f was designed to give about half the growth rate of H, with treatment M_f intermediate (Lewis *et al.*, 2002b and 2004).

weight increased and the overall relationship was clearly curvilinear. Figure 4 uses the same data but with log scales. The variation across weights was equalized and a roughly linear relationship found between the two variables. The fitted power function was $L = 0.3135 \times P^{1.850}$, where *L* is lipid weight and *P* is protein weight; the s.e. of the exponent was 0.0349. The considerable spread of the data around the trend lines in Figures 3 and 4 reflects mainly the systematic effects of line, sex and feeding treatment.

The lipid index, calculated as $L/P^{1.850}$, was reduced in the S compared with the C line, was lower in the males than in the females, and increased as the level of protein in the diet fell, as shown in Table 3 (in all cases, $P < 0.001$). It was not affected by the level of feeding.

Lipid content. Although the lipid index is the measure of fatness relevant for some modelling purposes, another

Table 4 *Main effects of level of feeding (H, M_f) by sex and slaughter point across lines on fatness (g lipid per kg empty body weight)*[†]

Sex	Feeding treatment[‡]	Slaughter point		
		SP3	SP4	SP5
Female	H	169.6	298.0	413.4
	M_f	151.1	280.7	421.9
Male	H	141.7	251.5	379.6
	M_f	139.9	261.2	329.8

[†]The three-way interaction was significant ($P < 0.01$); the s.e.d. for comparing any two cell means is 13.8 g/kg.
[‡]Described in Tables 1 and 3.

measure of fatness that can be used is lipid content, defined as lipid (g)/empty body weight (kg). The difference in lipid content between the two lines was estimated in 32 cases. The lines differed ($P < 0.001$) with means of 265.1 g/kg for C and 237.3 g/kg for S (s.e.d. 3.00 g/kg). Importantly, there was no interaction between line and feeding treatments ($P = 0.23$) even though these themselves produced very large differences ($P < 0.001$) as shown below.

There was an interaction between case and sex for fatness ($P < 0.05$), which was entirely due to the difference between the sexes increasing with the mean fatness. The females were 1.147 (s.e. 0.0194) times as fat as the males, with no effect of the feeding treatment on this ratio.

There was no effect of M_f compared with H on fatness except in males at SP5 (379.6 on H and 329.8 on M_f; s.e.d. 13.79; $P < 0.01$). The data are summarized in Table 4. When H was compared with L_f, there was no difference in lipid content (207.8 for H and 212.8 for L_f; s.e.d. 7.18; $P = 0.48$); however, this comparison was only at SP3 and SP4 because no animals were continued to SP5 on L_f.

The main effect of H *v.* L_p (Table 5) was significant as was their interaction with SP in the males ($P < 0.001$). The interaction arose because the lambs on L_p were fatter than those on H to a greater extent at SP3 (by 95.4 g/kg) than at SP4 (by 48.3 g/kg). The excess fattening due to L_p thus reduced in extent as the animals grew. On average, the fatness on M_p (281.3 g/kg) was greater ($P < 0.001$) than that on H (256.4 g/kg). The proportional extent to which fatness on M_p was greater than on H decreased ($P < 0.05$) with SP: 1.28 times at SP3, 1.14 times at SP4 and 1.01 times at SP5.

Energy content in relation to slaughter weight

Total energy content was regressed on slaughter weight for the two sexes of the two lines when fed H *ad libitum*. The values of the coefficients for the quadratic regressions are in Table 6 from which the energy content of gain can be calculated as illustrated for a weight of 40 kg.

Relationships between carcass and non-carcass chemical components

The proportion of the total chemical body as carcass, which increased steadily ($P < 0.001$) with weight, was from 0.580 (s.d. 0.020) kg/kg at SP3 to 0.674 (s.d. 0.017) kg/kg at SP5. The proportions of total protein (Figure 5a) and of total lipid (Figure 5b) that were in the carcass increased curvilinearly with weight ($P < 0.001$).

There was no line effect on the proportion of the total chemical body as carcass ($P = 0.34$). The S line had a higher proportion of its protein in the carcass than did the C line (0.627 *v.* 0.610; s.e.d. 0.0018; $P < 0.001$). For lipid, the difference was reversed (0.736 *v.* 0.744; s.e.d. 0.0024; $P < 0.05$). The line effects were consistent across sex and feeding treatment. The proportions of the body, body protein and body lipid in the carcass were higher in females than in males ($P < 0.01$); the ratios were 1.024, 1.017 and 1.017, respectively. There were no effects of level of feeding on these proportions ($P > 0.20$). The proportion of the body in the carcass was 1.026 times higher for the feeds of lower (M_p and L_p) as compared with higher (H) protein content ($P < 0.05$). For body protein, the equivalent ratio was 1.021 ($P < 0.05$). For body lipid, the ratio was 1.004, which was not significantly different from unity.

Table 5 *Main effects of level of protein (H, L_p) by line, sex and slaughter point (case) on fatness (g lipid per kg empty body weight)*[†]

Feeding treatment[‡]	Male				Female selection
	Selection		Control		
	SP3	SP4	SP3	SP4	SP4
H	118.2	212.0	132.9	235.1	252.5
L_p	215.3	278.0	226.6	286.9	279.5
L_p/H	1.82	1.31	1.71	1.22	1.11

[†]The main effects of feeding treatment and case were significant ($P < 0.001$); the s.e.d. for comparing any two case means is 11.6 g/kg. There was an interaction between feeding treatment and slaughter point in the males ($P < 0.001$).
[‡]Described in Table 1.

Table 6 *Polynomial regressions*[†] *of total energy content (TEC; MJ) on slaughter weight (SW; kg) by line and sex for animals fed H* ad libitum[‡]

Line	Sex	*a*	*b*	R^2	*dTEC/dSW* at SW = 40 kg[§]
Selection	Male	4.007	0.1107	0.980	12.86
	Female	5.438	0.1187	0.988	14.93
Control	Male	4.296	0.1192	0.993	13.83
	Female	5.483	0.1365	0.995	16.40

[†]$TEC = (a \times SW) + (b \times SW^2)$.
[‡]Feed H is described in Table 1. All regressions had a *P*-value <0.001.
[§]$dTEC/dSW = a + (2 \times b \times SW)$, MJ/kg gain.

Discussion

In order to implement the scheme illustrated in Figure 1, where the body is essentially constructed from its weight of protein and the energy supply, the constants and variables

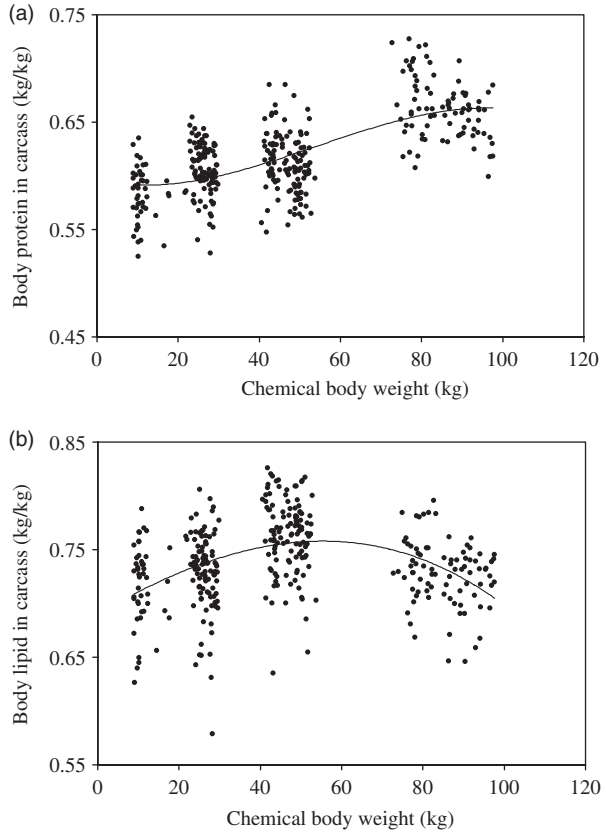

Figure 5 Relationship between the proportion of (a) body protein and (b) body lipid in the carcass (kg/kg) and chemical body weight (kg) across treatments. The third-order polynomial is shown.

need to be clearly evaluated. The stages of constructing the body are given below with particular reference to the consequences that might occur under genetic selection.

Composition of the lipid-free dry matter

As shown in Figure 1, the lipid-free dry matter consists of protein and 'other'. As expected, the protein content of the lipid-free dry matter was not affected by live weight, sex or feeding treatment. The null hypothesis that there would be no genetic line effect was formally rejected, although the difference was very small. The selected line value was 1.01 times that of the control. This may reflect the inclusion of ultrasonic muscle depth in the selection index, which would be expected to increase the muscle to bone ratio. A small increase in this ratio in the selection line was found by Lewis *et al.* (2002b and 2004) using the same animals.

Jenkins and Leymaster (1993) analysed the pelt-free empty bodies of sheep at weights of between 4.2 and 81.8 kg. Their lipid-free dry matter contained 0.751 kg/kg of protein in good agreement with our overall mean of 0.757 kg/kg. The suggestion that the protein content of the lipid-free dry matter is constant across a wide range of circumstances is broadly supported by our data but effects of selection are possible.

Water weight

Our assumption, made in agreement with others (e.g. Agricultural Research Council (ARC), ARC, 1981; Emmans and Kyriazakis, 1995), that water weight would be an exponential function of protein weight was confirmed (Figure 2). The value of the exponent, *b*, was not affected by line or sex. Although the value of the scalar, *a*, was not significantly affected by line or sex, the values were in agreement with the expectation that they would increase with the mature protein weight of the genotypes considered.

An alternative approach is to use the estimates of *a* for the four genotypes (two sexes by two lines), in combinations with estimates of their mature protein weights derived as described in the Material and methods, to estimate their individual values for the water : protein ratio at maturity. When this was done, the four estimates varied little around a mean of 3.45; all were within 1% of this value. The value of 3.45 is in good agreement with other estimates from sheep and other species (Blaxter *et al.*, 1982; Emmans, 1988; Emmans and Kyriazakis, 1995). Jenkins and Leymaster (1993) estimated their sheep to have 11.7 kg of protein and 38.6 kg of water in their pelt-free empty body at maturity (their Table 4), giving a mature water : protein ratio of 3.30.

The values of the two parameters in the power function relating water to protein in sheep, and in other species, are sensitive to the detailed methodologies used in slaughter, storage and chemical analysis. However, the underlying relationship does appear to be well described by a simple power function. The relationship between water and protein was not affected by level of feeding but the ratio was slightly increased as the protein content of the feed was reduced. It is possible that on low-protein feeds, the growth of tissues with higher than average water contents is favoured. A consequence would be that the animal would have more water than usual and this may have happened here.

Lipid weight and fatness

In non-limiting nutritional conditions, the weight of lipid in the body is often found to be a simple power function of the weight of protein for a given kind of animal (Emmans, 1988). The values of the two parameters can vary markedly between genotypes. An example for the effects of artificial selection in pigs is in Knap (2000). In our two lines of sheep, selection on a lean growth index (Simm and Dingwall, 1989) has reduced fatness as observed in this study. At the whole-body chemical level, females were fatter than males consistent with fat content as measured by dissection (Lewis *et al.*, 2002b and 2004).

Fatness at a weight is, however, sensitive to nutritional conditions. To make the assumption that the phenotypic fatness observed reflects the underlying genetic fatness can lead to misleading conclusions being drawn. Our data show that fatness in sheep can be substantially affected by the protein content of the feed used, in agreement with others

(NRC, 1985). The extent to which fatness was increased on the lower protein diets decreased as the animals grew, presumably because their protein requirement was falling. Although we found that fatness was reduced by a lower level of feeding in only one case – the males at SP5 – there is evidence that feed restriction can reduce fat content at a given weight in sheep (Blaxter *et al*., 1982) as has often been observed in swine (e.g. ARC, 1981).

Energy content

The fact that the relationship between the energy content of the chemical body and slaughter weight is of the quadratic form is consistent with the expression of Parks (1982) for the energy concentration in the body. Where energy requirements for growth are calculated from the energy content of the gain, the quantitative relationships given in Table 6 are needed. It is clear that the numerical values of the relevant coefficients vary with genetic line and sex. NRC (1985) linearly reduced the energy content of the gain at a live weight as the mature weight of ram used increased. As the mature weight of our selected line was greater than that of the control (Lewis *et al*., 2002a), the values in Table 6 are consistent with this suggestion but, in addition, the reduction in fatness resulting from selection would also have an effect.

Genetic line effects on distribution

The selection index increased the rate of lean deposition while restricting the rate of fat deposition (Simm *et al*., 2002). The only measures of body composition included in the index were ultrasonic muscle and fat depths spanning the *longissimus* muscle. While there was no direct selection for lean or fat distribution between carcass and non-carcass, it would be expected that, if anything, the selection used would move lean (and hence protein) into the carcass and fat (and hence lipid) away from the carcass. The results suggest that this has happened.

As expected, the relationship between protein and other non-lipid components of the dry matter was close to constant; it was unaffected by live weight, sex and feeding treatment, and only trivially by genetic line. The form of the relationship between protein and water was also unaffected by live weight and feeding treatment, with any differences due to sheep genotype explained by differences in mature body protein weight. The form of the relationship between protein and lipid was unaffected by genetic line and feeding treatment, but there were effects on the value of the scalar. The analyses and quantitative assessments given here thus allow the implementation of the scheme shown in Figure 1 for different kinds of sheep.

Acknowledgements

Financial support of the Meat and Livestock Commission and the Scottish Executive Environment and Rural Affairs Department is gratefully acknowledged. The authors are grateful to G. Simm and W. S. Dingwall for their long-term scientific investment in the SAC Suffolk flock, to M. Lewis for formulation of the diets, and for the technical assistance of the SAC staff.

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