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Feed intake of sheep as affected by body weight, breed, sex, and feed composition

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Feed intake of sheep as affected by body weight, breed, sex, and feed composition[1]

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ABSTRACT: The hypotheses tested were that genetic size-scaling for mature BW (A, kg) would reduce variation in intake between kinds of sheep and that quadratic polynomials on u = BW/A with zero intercept would provide good descriptions of the relationship between scaled intake (SI, g/$A^{0.73}$ d) and degree of maturity in BW (u) across feeds of differing quality. Both sexes of Suffolk sheep from 2 experimental lines (n = 225) and from 3 breed types (Suffolk, Scottish Blackface, and their cross; n = 149) were recorded weekly for ad libitum feed intake and BW; recording of intake was from weaning through, in some cases, near maturity. Six diets of different quality were fed ad libitum. The relationship between intake and BW on a given feed varied considerably between kinds of sheep. Much, but not all, of that variation was removed by genetic size-scaling. In males, the maximum value of SI was greater than in females ($P = 0.07$) and was greater in Suffolk than in Scottish Blackface, with the cross intermediate ($P = 0.025$); there was no difference between the 2 Suffolk lines used ($P = 0.106$). The quadratic polynomial model, through the origin, was compared with a split-line (spline) regression for describing how SI varied with u. For the spline model, the intercept was not different from zero in any case ($P > 0.05$). The values of u at which SI achieved its maximum value (u* and SI*) were calculated. Both models fit the data well; the quadratic was preferred because it predicted that SI* would be achieved within the range of the long-run data, as was observed. On a high quality feed, for the spline regression, u* varied little around 0.434 (SD = 0.020) for the 10 different kinds of sheep used. For the quadratic, the mean value of 0.643 (SD = 0.066) was more variable, but there were no consistent effects of kind of sheep. The values of u* and SI* estimated using the quadratic model varied among the 6 feeds: 0.643 and 78.5 on high quality; 0.760 and 79.6 on medium protein content; 0.859 and 73.3 on low protein content; 0.756 and 112 on a low energy content feed; 0.937 and 107 on ryegrass; and 1 (forced, as the fitted value of 1.11 was infeasible) and 135 on Lucerne. The value of u* tended to increase as feed digestibility decreased. We conclude that genetic size-scaling of intake is useful and that a quadratic polynomial with zero intercept provides a good description of the relationship between SI and u for different kinds of sheep on feeds of different quality. Up to u ≅ 0.45, intake was directly proportional to BW.

Key words: feed composition, feed intake, genetic size-scaling, selection, sex, sheep

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INTRODUCTION

Feed intake in a growing animal changes as its size increases. Pittroff and Kothmann (2001) reviewed 11 intake models. Animal size was present in all, but breed in only one. The models also used different expressions for animal size, including BW, $BW^{0.75}$, and $BW^{0.73}$.

Intake of different sheep breeds at a BW may vary with mature BW, called **A**. Taylor (1980) proposed 2 genetic size-scaling rules. The first was to treat all time variables, such as daily feed intake, as proportional to $A^{0.73}$. The second was to express BW as a proportion of A, **u** = BW/A. Scaled rates of intake were then re-

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Table 1. Composition of the feeds, as-fed or DM basis as indicated

Item	Feed[1] H	MedP	LP	LE	RG	LUC
Ingredient, g/kg as fed						
Barley	582.5	504.2	464.0	0.0	0.0	0.0
Dried grass	200.0	66.7	0.0	0.0	970.0	0.0
Dried Lucerne	0.0	0.0	0.0	0.0	0.0	970.0
Oatfeed	0.0	31.0	46.7	628.9	0.0	0.0
Citrus pulp	0.0	233.0	350.0	0.0	0.0	0.0
Sugar beet pulp	0.0	0.0	0.0	110.0	0.0	0.0
Soya-bean meal	70.0	34.4	16.7	180.0	0.0	0.0
Fish meal	60.0	20.0	0.0	0.0	0.0	0.0
Molasses	50.0	63.0	70.0	50.0	0.0	0.0
Protected fat	0.0	11.0	16.6	0.0	0.0	0.0
Minerals/vitamins	37.5	36.7	36.0	31.1	30.0	30.0
Chemical composition						
DM,[2] g/kg	892	882	878	923	958	939
CP, g/kg of DM	192	141	120	130	135	182
NDF, g/kg of DM	242	228	212	595	493	449
AHEE,[3] g/kg of DM	26	30	28	14	32	36
Ash, g/kg of DM	87	81	73	73	103	103
NCGD,[4] g/kg	789	826	845	430	654	576
IOM,[5] g/kg of DM	103	71	65	483	238	321
ME, MJ/kg of DM	11.7[6]	12.3[6]	12.5[6]	6.4[6]	9.5[7]	8.3[7]

[1]Feed: high quality (H), medium (MedP), and low (LP) protein content; low energy (LE) content; ryegrass (RG); and Lucerne (LUC). All feeds were pelleted.

[2]Based on weekly determinations.

[3]Acid-hydrolyzed ether extract.

[4]Neutral cellulase gamanase digestibility.

[5]Indigestible OM, calculate as IOM = [1,000 – ash – (ME/14.5)].

[6]Predicted from 0.014 × NCGD + 0.025 AHEE (Thomas et al., 1988).

[7]Predicted from 0.0154 × NCGD − 0.59 (Givens et al., 1992), which is germane for a food composed of a single forage.

lated to u. This scaling allows the data from different breeds to be more sensibly compared; genetic variation in intake scaled in this way may still exist. The quantitative form of the relationship between intake (appropriately scaled) and u is not obvious and is treated in very different ways by the models reviewed by Pittroff and Kothmann (2001). For feeds that allow potential growth to be realized, Emmans (1997) proposed the form of the relationship between the 2 variables using body protein rather BW as the scalar; it had a maximum at $u \leq 1$. The function of Parks (1982) predicts that intake will reach its maximum at maturity, as does any function that makes intake proportional to BW^k.

Actual intakes for different kinds of sheep over a range of BW on different feeds will be presented here. These may be used to test models of feed intake. The hypotheses we used to test them were 1) that genetic size-scaling would reduce the variation in intake between sheep breeds or lines, 2) that a quadratic polynomial with zero intercept would provide a good description of the relationship between scaled intake (**SI**) and u for a high quality feed, 3) that for feeds that limited growth rate, a similar description would be applicable but with different values of the parameters, and 4) that intake would be directly proportional to BW up to about one-half mature size.

MATERIALS AND METHODS

The Animal Experiment Committee at the Scottish Agricultural College approved all procedures and protocols used in the experiments.

Animals and Feeds

The data were collected over the 5-yr period from 1994 through 1998 at the Scottish Agricultural College in Edinburgh. The material used has been fully described by Lewis et al. (2002, 2004a,b) and Macfarlane et al. (2004). The compositions of the feeds used are in Table 1. The numbers of sheep, their breed or line, and their estimated mature weights are shown in Table 2. Roughly one-half of the sheep were females and one-half were intact males.

In 1994, 1995, and 1996, both sexes of Suffolk sheep from 2 genetic lines were used. One line was selected for lean growth rate ($\mathbf{S_s}$), and other was its control ($\mathbf{S_c}$); details are in Simm and Dingwall (1989) and Simm et al. (2002). In these 3 yr, animals left the experiment for slaughter at prescribed BW so that the amount of data per animal varied substantially. In 1997 and 1998, both sexes of 3 breed types were used: purebred Suffolk (**S**), purebred Scottish Blackface (**B**), and their reciprocal

Table 2. The numbers of sheep by genotype and feed offered, with estimated mature weights

	Feed[2]							Mature weight, kg	
Breed type[1]	H	MedP	LP	LE	RG	LUC	Total	Female	Male
S_s	145	40	10	0	0	0	195	107[3]	132[3]
S_c	80	40	10	0	0	0	130	103[3]	116[3]
S	15	0	0	14	12	8	49	100[4]	130[4]
X	18	0	0	16	11	10	55	88[4]	114[4]
B	12	0	0	12	11	10	45	69[4]	90[4]
Total	270	80	20	42	34	28	474		

[1]The breed types were Suffolk selection (S_s) and control (S_c) lines, commercial purebred Suffolk (S), commercial purebred Scottish Blackface (B), and their reciprocal crosses (X).

[2]Feeds: high quality (H), medium (MedP), and low (LP) protein content; low energy (LE) content; ryegrass (RG); and Lucerne (LUC). All feeds were pelleted.

[3]Estimated using experimental data in this paper (Table 3).

[4]From Lewis et al. (2004a).

crosses (**X**). Within year, these animals were progeny of 4 rams per breed, purchased from distinct flocks, and mated to ewes acquired from 4 different flocks in each breed. No differences in performance between the reciprocal crosses were detected (Lewis et al., 2004a; Macfarlane et al., 2004), and thus the 2 groups were combined. In these 2 yr, all animals were grown to 0.65 of their predicted mature weight (Table 2).

Lambs were weaned at about 0.2 of their mature weight, group penned, and offered free access to a high protein (192 g of CP/kg of DM), high energy (11.7 ME of MJ/kg of DM) creep feed. Once a lamb was 2 kg more than its target weaning weight, it was shifted to an individual pen (1.52 × 1.40 m) with slatted floors and, where prescribed, gradually shifted to a new diet over the next week. Weekly records of intake were started at this time.

Six pelleted diets of different quality were fed (Table 1). One diet was defined as high quality (**H**; 192 g of CP/kg of DM CP; 11.7 MJ of ME/kg of DM). Two diets differed from H in protein, having medium (**MedP**; 141 g of CP/kg of DM CP) or low (**LP**; 120 g of CP/kg of DM CP) protein content, although similar energy contents. A fourth diet had low energy (**LE**; 6.4 MJ of ME/kg of DM) and low protein (130 g of CP/kg of DM CP) content. The remaining diets were pelleted ryegrass (**RG**) and Lucerne (**LUC**).

Animals were fed twice daily (at 0830 and 1530 h) with a feed allowance such that there were always refusals. Samples of the feed offered and bulked refusals were analyzed for DM weekly. Although the feed refused had less DM content than that offered, the difference was negligibly small in all cases. Intakes are reported on an as-fed basis. Lambs were offered 150 (1994, 1995, and 1996) or 75 g (1997 and 1998) of poor quality hay at each morning feeding. Almost all animals ate their hay allowance in almost all weeks. The reported feed intakes exclude hay.

Temperatures within the shed were recorded as weekly maximum and minimum values at 4 locations. The monthly average temperature increased from 7°C in March to 16°C in July, and then fell steadily to 5°C in December, with little variation between years. All of these temperatures were judged to be within the thermoneutral zone for fully fleeced sheep.

Statistical Methods

The primary data were the weekly BW and feed intakes of each animal. Although it is useful to see how intake varies with time, there may be more generality in expressing intake in relation to BW. To do this, each weekly rate of feed intake was related to mean BW in that week, calculated as the average of the beginning and end BW for the respective week. Following Taylor (1980), estimated mature BW, A (kg), was used for scaling. Scaled intakes were defined as intake (g/d), divided by $A^{0.73}$; u was used as a measure of scaled size. The estimates of A are shown in Table 2.

For a given breed or line on a given feed, intake was plotted against mean BW for each individual animal. The records were scanned to identify animals with exceptionally small intakes that were necessarily associated with slower growth rates. Only 2 animals out of 474 were so identified, both Scottish Blackface females; their entire records were excluded.

A quadratic function, with zero intercept, was used to describe the relationship between intake (**I**; g/d) and mean BW (kg). The justification for using this form is given in the Appendix. It allows estimation of the maximum intake, actual (**I***) or scaled (**SI***), and the BW or degree of maturity at which this occurred, BW* or **u***.

A second model tested was based on the finding of Emmans and Friggens (1995) that SI was directly proportional to u up to a particular value and then increased no further as u increased, within the range they used. We fitted a split-line (spline) regression to I on BW data, with the assumption that the right-hand line was horizontal. It had 3 parameters: the intercept, and 2 values that defined the breakpoint. The value of the x-variate at the break was BW*, and that of the y-variate I*. The values of these parameters were estimated for each individual animal to test whether there were differences due to sex or breed type. The regressions of SI on u were also fitted for the spline model. In this case, the 2 parameters that define the breakpoint were u*, the x-variate, and SI*, the y-variate.

Intakes on a Nonlimiting Feed (Feed H)

Data from the Selected and Control Lines of Suffolk. The relationship between I and BW is likely to be affected by sex and line. We tested whether these differences were consistent with genetic size-scaling rules of Taylor (1980). For the 2 lines by 2 sexes groups that contributed the longest runs of data, both the polynomial and spline models were fitted. The groups were 20 S_s and 10 S_c males recorded between about 25 and 113 kg of BW, and 10 S_s and 10 S_c females recorded between about 22 and 100 kg of BW. The animals had 41 (SD = 7) wk of intake data. Differences between individuals within a group, and the variation around the function for any one individual, were also investigated.

For these 50 animals, A was estimated from their BW by time (t) data to allow intake and BW to be appropriately scaled for each individual. This was done by estimating the 3 parameters of a Gompertz growth function (Gompertz, 1825) in the form

$$BW = A \times \exp\{-\exp[G_0 - (B \times t)]\}, \quad [1]$$

where A is mature weight and B is the rate parameter. The third parameter, G_0, is a transformed initial BW given by $G_0 = \ln[-\ln(BW_0/A)]$, and BW_0 is the BW at t = 0. To aid estimation, weekly data on BW from near birth to the start of feed recording were added to those existing for the period of feed recording. The average number of weeks per sheep with BW data was 49 (SD = 8) wk.

Data from Suffolk, Scottish Blackface, and Their Cross. Similar analyses were undertaken with these data. However, SI and BW were calculated using the group mean values for mature weight in Table 2.

Intakes on Limiting Feeds

For LE and the feeds of medium and low protein content, growth of the animals was reduced compared with that seen on feed H in the same experiment. The same was probably the case for RG and LUC, although this was not tested directly in the same experiment (Lewis et al., 2004a; Macfarlane et al., 2004).

The longest run set of data [46 (SD = 6) wk] for a limiting feed was that for the 4 line-sex combinations on feed MedP, with 5 animals per group (in total, 20 animals). Another 40 animals, 10 per group, were kept for 18 (SD = 4) wk, and yet another 20 animals, 5 per group, for 6 (SD = 1) wk, on this feed. The LP data used came from 10 males from each of S_s and S_c, one-half of which were recorded for 22 (SD = 4) wk and the other one-half for 9 (SD = 3) wk.

The mean estimates of A for males and females of S_s and S_c obtained from the animals on feed H grown to near maturity were also used to scale the data from the animals on MedP and LP. The quadratic polynomial with zero intercept was used to estimate SI over a range of u for all limiting feeds. These estimated intakes were expressed as a ratio to the estimated intake of H of like animals. The ratio was examined to see if it varied systematically with u and kind of animal. In the nature of the variable, itself based on a series of estimates, no formal statistical test of any effects was possible or sensible. All analyses were conducted using GenStat (VSN International, Hemel Hempstead, UK).

RESULTS

Intakes on a Nonlimiting Feed (Feed H)

Intake vs. BW. In Figure 1, intake is plotted against BW using all of the data from the 20 Suffolk S_s males. The overall fitted quadratic polynomial with intercept zero is shown. The R^2-value was 0.611 with a residual SD (**RSD**) of 345 g/d. The maximum estimated intake of 2,927 g/d occurred at a BW of 83.3 kg. Separate quadratic polynomials were fitted for the 20 individuals, again omitting the intercept. The R^2-value increased greatly to 0.838 with an RSD of 223 g/d indicating that much of the variation in Figure 1 was due to real differences between individuals. The fitted regression for animals with the greatest and least intakes at a BW of 60 kg is plotted to illustrate the extent of this variation between individuals. An average maximum feed intake among the 20 animals of 3,021 ± 72 g/d was estimated to occur at a BW of 87.3 ± 3.1 kg.

The spline model fitted to these same data had a slightly smaller RSD (340 vs. 345 g/d) than the quadratic polynomial. Figure 1 shows the fit of this model to the overall data. The average of the intercept (−66 ± 113 g/d) from the fit of the individual regressions for the 20 animals did not differ from zero ($P > 0.5$). The average maximum feed intake of 2,886 ± 67 g/d was estimated to be reached at an average BW of 57.6 ± 2.1 kg.

The data from the 50 Suffolk sheep (both sexes of 2 lines) kept to near maturity were used to test for line and sex effects on feed intake. When feed intake was regressed on mean BW using the spline model, the average of the intercept (−59 ± 82 g/d), from the fit of the individual regressions for the 50 animals, did not differ from zero ($P > 0.5$). The BW* and I* are shown in Table 3. For the quadratic and the spline models, both parameters were greater in males ($P < 0.01$) and in S_s ($P < 0.04$), but with no interaction ($P > 0.16$).

The data from the 6 breed type-sex combinations (both sexes of S, B, and X; n = 43) were used to test for differences in relationships between BW and intakes for these groups. The quadratic fits of weekly intakes against mean BW for the 6 groups are shown in Figure 2a. The spread around the individual lines (not shown to avoid cluttering in this and all subsequent figures) was similar to that seen in Figure 1. The 6

Table 3. Values of the parameters of the quadratic (Quad) and spline models from the regression of intake on BW, by line and sex, for Suffolk sheep on nonlimiting food (H)[1]

			BW*,[2] kg		I*,[2] g/d	
Line	Sex	No.	Quad	Spline	Quad	Spline
Selection	Male	20	87.2	57.6	3,021	2,886
	Female	10	70.0	46.6	2,406	2,297
Control	Male	10	75.4	49.3	2,745	2,556
	Female	10	65.1	46.7	2,225	2,049
Maximum SE			3.1	3.1	81.9	83.9
P-value						
Line			<0.001	0.038	<0.001	<0.001
Sex			<0.001	0.011	<0.001	<0.001
Line × sex			0.235	0.155	0.539	0.608

[1]Feed H is defined in Table 1.

[2]The maximum intake (I*), and the BW (BW*) at which this occurred (quadratic model) or was reached (spline model).

lines are clearly separated. Scaling for differences in mature weights reduced the degree of spread among groups (Figure 2b).

For the quadratic model, S sheep had greater values ($P < 0.001$) than B for BW* and I*, with X being intermediate (Table 4). The males had greater values for both parameters than females, but only for I* was this difference significant ($P = 0.025$).

The spline model was also fit using individual animal intake and BW data from the 6 breed type-sex combinations on feed H. The intercept was not different from zero ($P > 0.05$). The males had greater ($P < 0.001$) values for both parameters than females. The S sheep had greater values ($P < 0.001$) than B for BW* and I*, with X being intermediate.

Estimating Mature Size. For all 50 Suffolk animals grown to near maturity, the nonlinear fit of the Gompertz growth function converged. The fit was good with a mean RSD of 1.7 kg. The parameter values are reported in Table 5 by line and sex.

Scaling Intake for Mature Size. The estimate of A for each of the S_s male animals (n = 20) was used

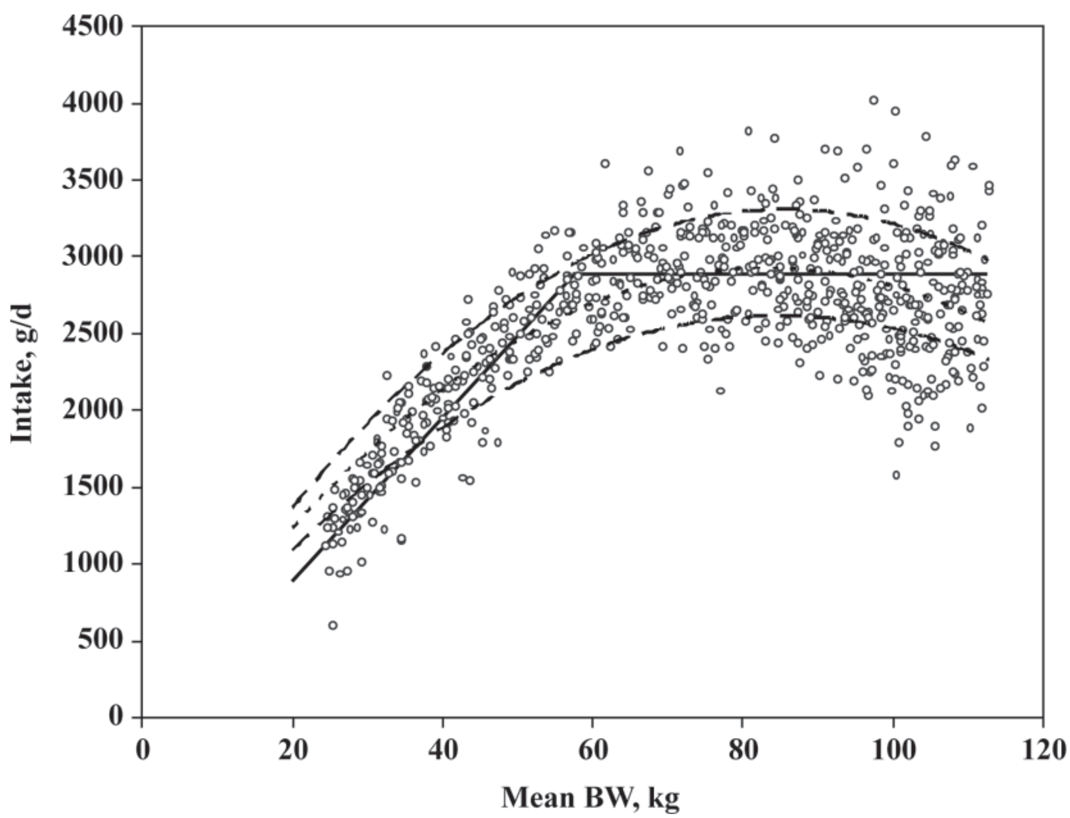

Figure 1. Intake (g/d) plotted against BW (kg) for 20 male Suffolk animals from the selection line fed the high quality diet to near maturity. The fit of the overall quadratic polynomial is shown (dotted line), along with those for the animals with greatest and least predicted intakes at 60 kg of BW (dashed lines). The fit of the spline model is also shown (solid line).

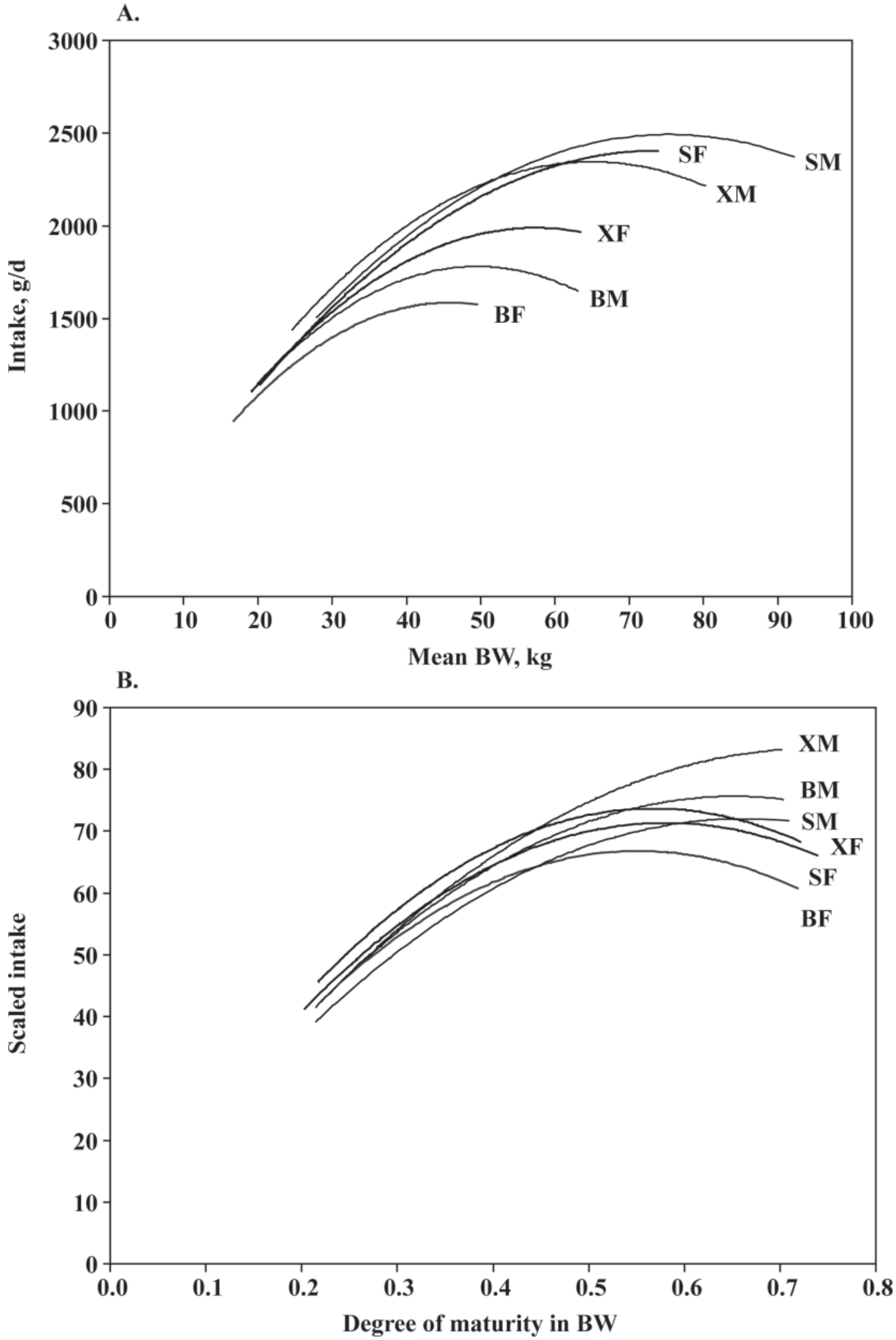

Figure 2. A) Intake (g/d) plotted against BW (kg) for 3 breeds [Suffolk (S), Scottish Blackface (B), and their reciprocal cross (X)] in males (M) and females (F) fed the high quality diet to 0.65 mature size. The fits of the quadratic polynomials are shown. B) Scaled intake (g/$A^{0.73}$ d, where A is mature weight in kg) plotted against degree of maturity in BW for 3 breeds (S, B, and X) in males (M) and females (F) fed the high quality diet to 0.65 mature size. The fits of the quadratic polynomials are shown.

to produce values of u and SI. The variation between animals was reduced only slightly as compared with the unscaled data, as indicated by only a small increase in the R^2-value from 0.611 to 0.661 for the fit of the quadratic polynomial.

When SI was regressed on u using the spline model, the average of the intercept (-1.7 ± 2.7 g/$A^{0.73}$ d), from the fit of the individual regressions for the 50 Suffolk animals, did not differ from zero ($P > 0.5$). The values of u* for both the quadratic and spline models

Table 4. Values of the parameters of the quadratic (Quad) and spline models for the regression of intake on BW, for both sexes of Suffolk and Scottish Blackface sheep, and their cross, on nonlimiting feed (H)[1]

			BW*,[2] kg		I*,[2] g/d	
Breed	Sex	No.	Quad	Spline	Quad	Spline
Suffolk	Male	6	82.3	57.4	2,623	2,497
	Female	9	79.6	46.5	2,568	2,353
Cross	Male	8	66.2	46.0	2,393	2,347
	Female	10	58.8	38.8	2,055	1,989
Blackface	Male	5	49.5	36.0	1,858	1,819
	Female	5	41.7	29.7	1,569	1,541
Maximum SE			7.4	2.4	143	100
P-value						
Breed			<0.001	<0.001	<0.001	<0.001
Sex			0.257	<0.001	0.025	<0.001
Breed × sex			0.907	0.521	0.441	0.412

[1]Feed H is defined in Table 1.
[2]The maximum intake (I*), and the BW (BW*) at which this occurred (quadratic model) or was reached (spline model).

are shown in Table 6. The value for the spline model (0.439 ± 0.015) was not affected ($P > 0.68$) by line or sex, but was appreciably less than that estimated by the quadratic model (0.649 ± 0.0083), which also was not affected by line or sex ($P > 0.20$). The value of SI* assessed using the quadratic model was affected by sex ($P < 0.001$), with the male value of 85.6 substantially greater than that of the female of 77.5, but not by line ($P = 0.106$). When assessed using the spline model, SI* was also greater in males (80.7 vs. 72.6; $P < 0.001$). With this model, SI* was also greater in the selection line (78.9 vs. 74.4; $P = 0.009$).

For the quadratic model, the value of u* (Table 7) was greater in S than in B, with X intermediate ($P = 0.044$), and in the females than in the males ($P = 0.030$). The SI* values were greater in S than in B, with X intermediate ($P = 0.025$). Scaled intake in the females was slightly greater than that in the males [79.5 vs. 73.4 (maximum SE = 2.6) g/$A^{0.73}$ d; $P = 0.071$].

The spline model was fitted using individual animal intake and BW data (scaled to a group mature weight) for both sexes of the 3 breed types on feed H. As found with the unscaled case, the intercept was not different from zero with scaling ($P > 0.05$). There were no effects of breed or sex ($P > 0.088$) on u* (Table 7), with an overall mean of 0.430 ± 0.0092. There were breed effects ($P = 0.049$) on the SI* at this u*, with S scaled intake greatest and B least.

Intakes on Limiting Feeds

Protein Level. For males, averaged across genetic line, the quadratic fits for SI of H, MedP, and LP against u in BW are shown in Figure 3. Females are not shown; there were no females from the control line on feed LP. For H, MedP, and LP, SI* values were estimated by the quadratic equations to be 82.3, 79.6, and 73.3 g/$A^{0.73}$ d at u* values of 0.645, 0.760, and 0.859, respectively.

LE Feed and Forages. The quadratic fits of I to BW for LE for the 6 groups are shown in Figure 4a, and of the SI to u in Figure 4b. Maximum SI and u* increased in the order B, X, and S, and were greater in males than in females. However, there were no clear

Table 5. Main Gompertz growth parameters in Suffolk sheep grown on a nonlimiting feed (H) to near maturity[1]

			Mature size (A; kg)		Rate (B × 1,000; d^{-1})		Scaled rate (B*)[3]	
Line[2]	Sex	No.	Mean	SD	Mean	SD	Mean	SD
S_s	Male	20	131.8	12.7	9.55	1.8	0.0355	0.0059
	Female	10	106.8	6.9	9.94	1.4	0.0350	0.0046
S_c	Male	10	116.2	3.2	10.12	1.2	0.0365	0.0042
	Female	10	103.5	8.4	8.52	1.6	0.0297	0.0055

[1]The function fitted was $BW = A \times \exp\{-\exp[G_0 - (B \times t)]\}$, where A is mature weight and B is the rate parameter. The third parameter, G_0, is a transformed initial BW given by $G_0 = \ln[-\ln(BW_0/A)]$ and BW_0 is the BW at t = 0. Feed H is defined in Table 1.
[2]Lines were Suffolk selection (S_s) and control (S_c).
[3]$B^* = B \times A^{0.27}$.

Table 6. Values of the parameters of the quadratic (Quad) and spline models from the regression of scaled intake (SI) on degree of maturity in BW (u), by line and sex, for Suffolk sheep on nonlimiting feed (H)[1]

			u*[2]		SI*,[2] g/$A^{0.73}$ d	
Line	Sex	No.	Quad	Spline	Quad	Spline
Selection	Male	20	0.662	0.438	85.8	81.9
	Female	10	0.656	0.436	79.6	75.9
Control	Male	10	0.649	0.425	85.4	79.9
	Female	10	0.629	0.457	75.4	69.2
Maximum SE			0.018	0.031	2.2	2.2
P-value						
Line			0.197	0.910	0.106	0.009
Sex			0.452	0.678	<0.001	<0.001
Line × sex			0.677	0.556	0.363	0.307

[1]SI is g/$A^{0.73}$ d and u is degree of maturity in BW (u = BW/A), where A is mature BW (kg). Feed H is defined in Table 1.

[2]The maximum scaled intake (SI*), and the degree of maturity (u*) at which this occurred (quadratic model) or was reached (spline model).

effects of breed or sex on SI* (111.8 g/$A^{0.73}$ d) or on u* (0.756).

The plots of I and SI against BW and u, respectively, for RG and LUC are not shown. They were very similar in form to the plots for LE in Figures 4a and 4b for the 6 breed-sex groups. The fit of the quadratic regressions of SI on u for H, LE, RG, and LUC, averaged across the groups, is shown in Figure 5. Intakes were much greater on LUC and LE than on H, with RG intermediate. The statistics of the regressions are in Table 8. The R^2-values were greatest for RG and LUC, and least for H. The value of u* increased from 0.627 on H, to 0.756 on LE, and to 0.937 on RG. For LUC, intake was estimated to peak beyond a u of 1. However, the estimated SI* of 136.7 was only slightly greater than the predicted intake at u equals 1 of 135.4 g/$A^{0.73}$ d.

The SI of diets MedP, LP, LE, RG, and LUC, as proportions of those on H, are plotted against u in Figure 6. Scaled intake on MedP increased from 0.85 of that on H at u = 0.20 to 1.00 at u = 0.80. The pattern was general across Suffolk lines and sexes. The ratio of SI on LP to that on H was always less than 1 and decreased somewhat as u increased over the range considered (Figure 6). The sheep on LE always ate more feed than those on H. The ratio of the estimated SI on LE relative to H increased overall from 1.3 at u = 0.20 to 1.5 at u = 0.65. Initially, intake was similar on RG and H, but the ratio of SI of RG to that of H increased steadily to 1.3 at u = 0.65 (Figure 6). For LUC, the ratio of SI to that of H increased steadily with u from 1.1 at u = 0.20 to 1.5 at u = 0.65. Intake of LUC was on average 1.1 times that of RG.

Table 7. Values of the parameters of the quadratic (Quad) and spline models from the regression of scaled intake (SI) on degree of maturity in BW (u), for both sexes of Suffolk and Scottish Blackface sheep, and their cross, on nonlimiting feed (H)[1]

			u*[2]		SI*,[2] g/$A^{0.73}$ d	
Breed	Sex	No.	Quad	Spline	Quad	Spline
Suffolk	Male	6	0.633	0.441	75.1	71.5
	Female	9	0.796	0.465	89.0	81.6
Cross	Male	8	0.579	0.402	75.2	73.8
	Female	10	0.669	0.441	78.2	75.7
Blackface	Male	5	0.552	0.402	69.8	68.3
	Female	5	0.607	0.431	71.3	70.0
Maximum SE			0.068	0.026	5.0	3.6
P-value						
Breed			0.044	0.183	0.025	0.049
Sex			0.030	0.088	0.071	0.068
Breed × sex			0.657	0.932	0.296	0.305

[1]SI is g/$A^{0.73}$ d and u is degree of maturity in BW (u = BW/A), where A is mature BW (kg). Feed H is defined in Table 1.

[2]The maximum scaled intake (SI*), and the degree of maturity (u*) at which this occurred (quadratic model) or was reached (spline model).

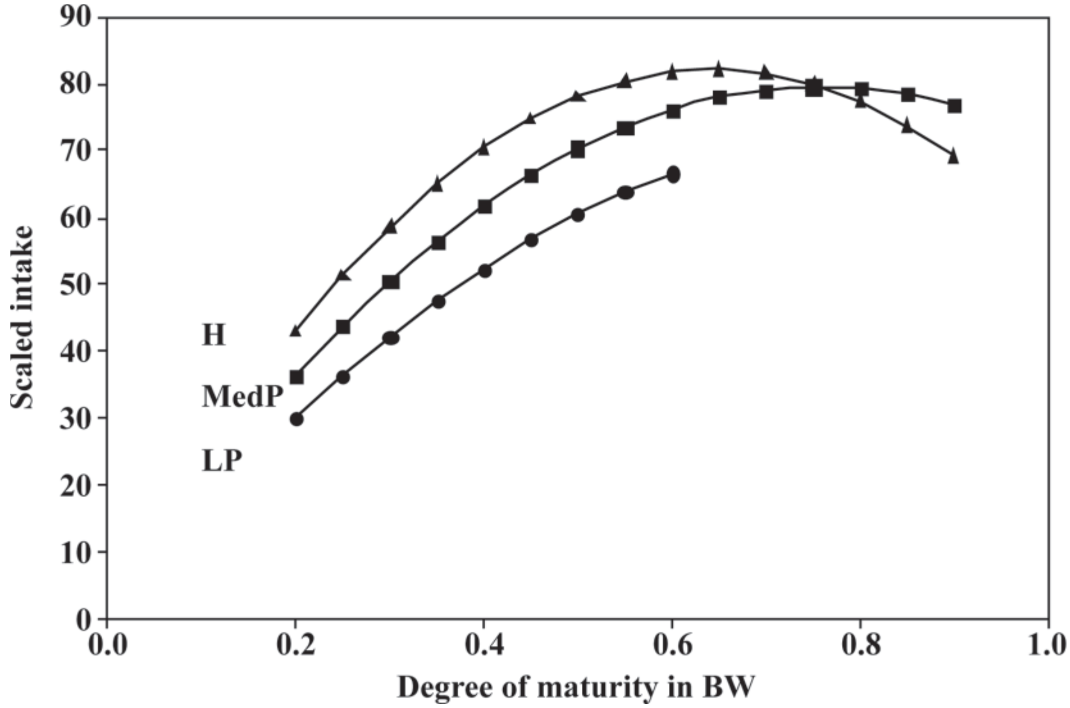

Figure 3. Scaled intake (g/$A^{0.73}$ d, where A is mature weight in kg) plotted against degree of maturity in BW for the average of male selection and control line Suffolk on high quality (H; ▲), medium (MedP; ■), or low (LP; ●) protein content feeds. The fits of the quadratic polynomials are shown.

DISCUSSION

Relating Intake to BW and Genetic Size-Scaling

It is usual to relate intake to BW (ARC, 1981; NRC, 1987, 2007; Pittroff and Kothmann, 2001). However, only if animals differing in mature size eat the same amount at the same BW is it justified to ignore differences in mature size. The evidence presented here is that they do not. By using the genetic size-scaling rules of Taylor (1980), we substantially reduced the amount of variation present, even within the single species of sheep. We therefore focus hereafter on differences in intakes that have been appropriately scaled.

The exact form of the equation relating the degree of maturity in BW, u, of an animal and its rate of intake is unclear, although it is expected to be similar for breed types of different mature size. For feeds that do not limit the growth of the animal, it is possible to predict the relationship between size and intake by calculating the requirement for the first limiting feed resource. Emmans (1997) provides the equations for the solution where energy is that resource. Although the quantitative relationship between SI and u in such conditions is expected to vary with the growth and fattening characteristics of the animal, there is some generality in the form. Intake is predicted to increase with u to a maximum value at an intermediate value of u, and then to fall somewhat as the animal grows toward maturity. For many simulated cases we have found that a quadratic function with zero intercept gives an excellent, although not perfect, description as indicated in the Appendix.

Up to about 0.5 maturity, intake was found to be almost directly proportional to u (i.e., for a given breed type), intake equals k × $BW^{1.0}$, where the value of k will vary between kinds of animals on a given feed, and between feeds for a given kind of animal. Intake then changes little as u increases further up to about 0.8. For this reason, the spline model was found to give almost as good a fit as the quadratic function, at least where the data were for values of $u < 0.7$.

Taylor (2009), using pre-1970 published data on the feed intake of 8 mammalian species over the postnatal growth period, found that the curves of SI (in MJ of ME) against u were all somewhat similar in shape. Only 1 had an immature maximum. The average intake curve was described by $0.81[1.02 - \exp(-4u^{1.4})]$, which increases to a maximum of 0.81 at u equals 1. Any rule that makes intake a constant function of BW^k will also have this property. The function is similar in shape to that of Parks (1982), except that the rate of intake is related to time rather than BW; it also predicts a maximum rate of intake when u equals 1. For almost all of our data, with LUC the one exception, SI was found to have a maximum value when u was less than 1. The quadratic form of function allows this, although the maximum will not inevitably be predicted to occur within the feasible range.

We used 2 models to estimate the degree of maturity at which maximum intake was either attained (spline model) or occurred (quadratic model), called u*. When the spline model was used to estimate the value of u*

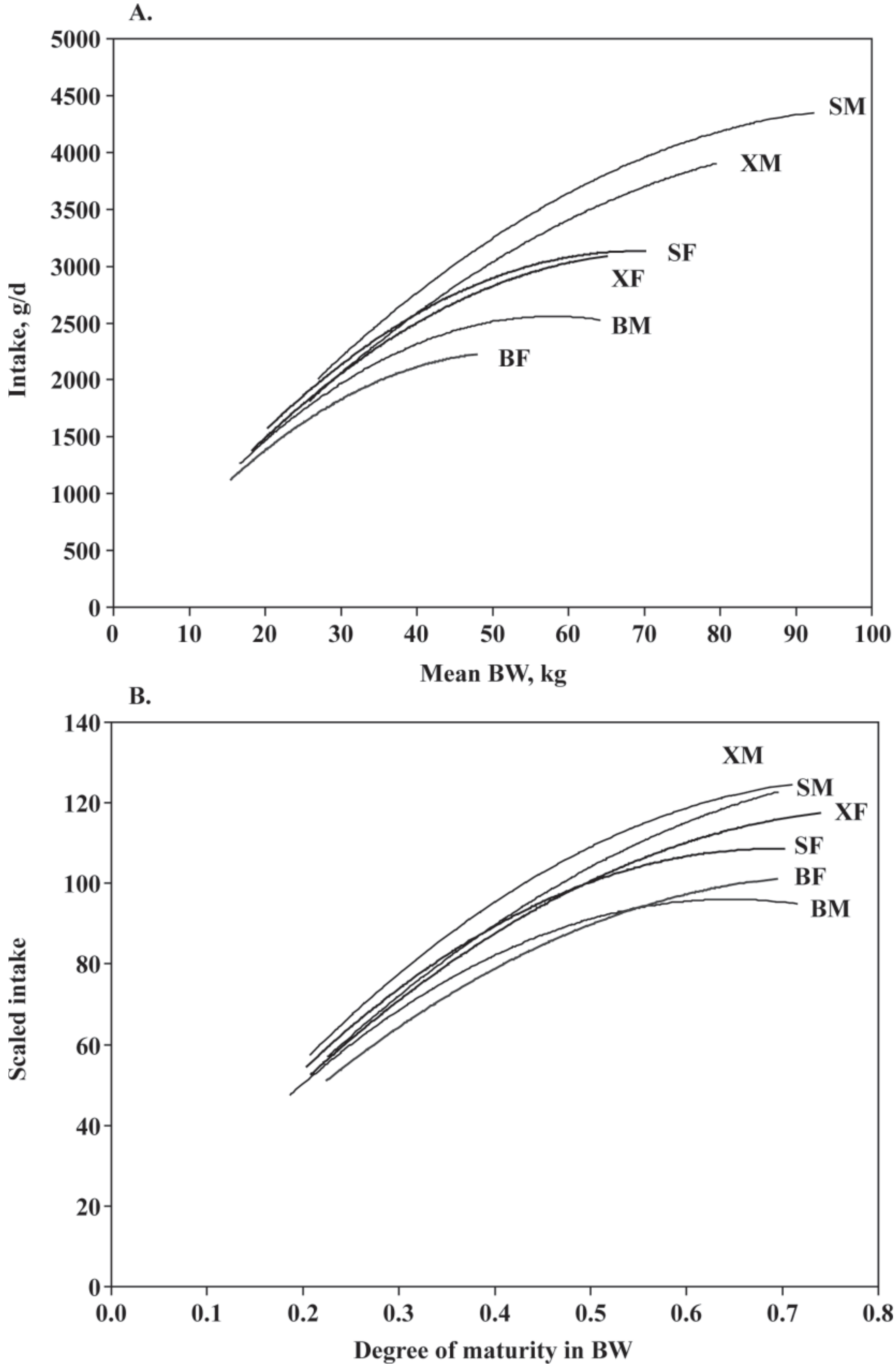

Figure 4. A) Intake (g/d) plotted against BW (kg) for 3 breeds [Suffolk (S), Scottish Blackface (B), and their reciprocal cross (X)] in males (M) and females (F) fed the low energy content diet to 0.65 mature size. The fits of quadratic polynomials are shown. B) Scaled intake (g/$A^{0.73}$ d, where A is mature weight in kg) plotted against degree of maturity in BW for 3 breeds (S, B, and X) in males (M) and females (F) on low energy content to 0.65 mature size. The fits of quadratic polynomials are shown.

directly, there were no effects of line or sex for the Suffolk sheep on feed H. The value of u* estimated by the quadratic model using individual values was also unaffected in the same sheep. However, the differences between the models in estimating this point are shown by the overall means of 0.439 ± 0.015 for the spline as

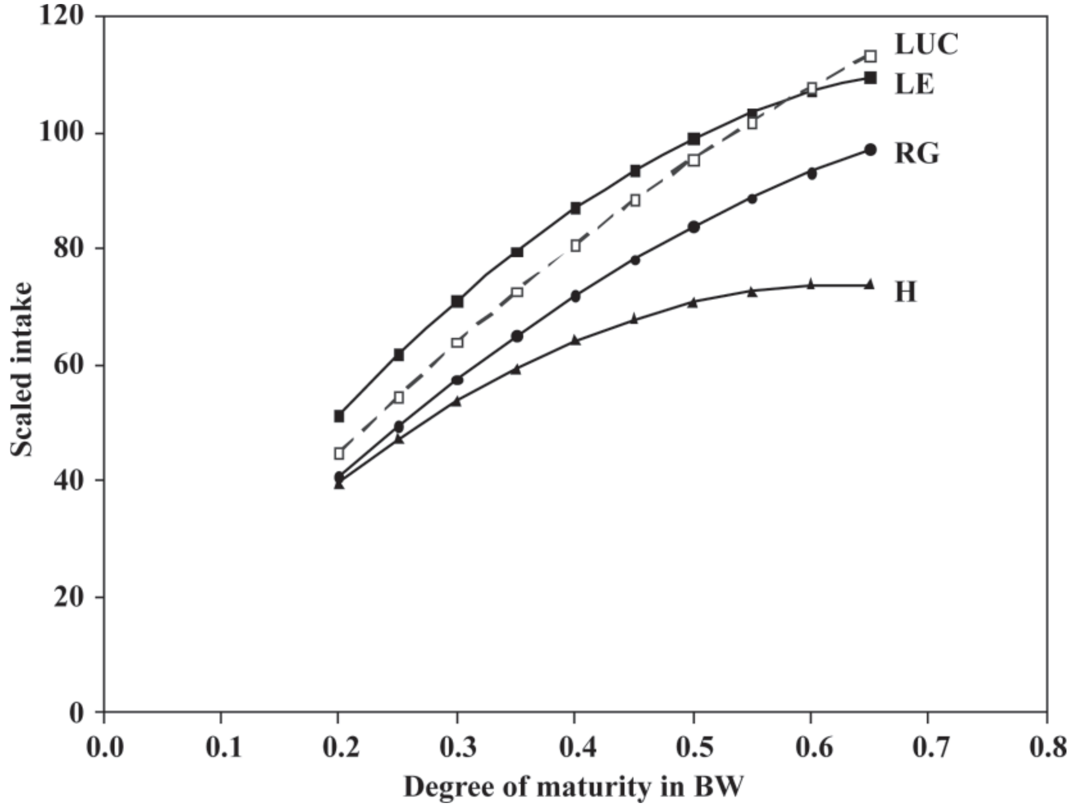

Figure 5. Scaled intake (g/$A^{0.73}$ d, where A is mature weight in kg) plotted against degree of maturity in BW for the average of males and females of 3 breeds (Suffolk, Scottish Blackface, and their reciprocal cross) fed high quality (H; ▲), low energy content (LE; ■), ryegrass (RG; ●), and Lucerne (LUC; □) diets. The fits of quadratic polynomials are shown.

compared with 0.649 ± 0.0083 for the quadratic. The estimate based on the fit of the quadratic form is the more sensible.

When considering the 3 breeds of 2 sexes, the value of u* for feed H using the spline model was unaffected by either factor. The overall mean of 0.430 ± 0.0092 was similar to that seen for the same feed in both sexes of the 2 lines of Suffolk considered alone. However, when u* was estimated using the quadratic model, there were significant effects of breed and sex, showing that u* is not constant across breeds; this conclusion is contrary to that reached when the spline model was used. The lack of constancy in the value of u* was further emphasized by the large differences in its value for the different feeds. Across the 6 feeds used, the value of u* tended to increase as the digestibility of the feed decreased.

There is no reason a priori to expect intake to vary directly with BW^z, where z has a value such as 0.75. It

Table 8. Quadratic regressions of scaled intake (SI) on degree of maturity in BW (u) for 4 feeds across the 6 breed-sex combinations[1]

	Feed[2]			
Statistic	H	LE	RG	LUC
Linear	235.4 ± 3.33	295.7 ± 4.35	228.4 ± 3.09	246.2 ± 4.28
Quadratic	−187.7 ± 5.82	−195.5 ± 7.88	−121.9 ± 5.80	−110.9 ± 7.67
R^2	0.485	0.611	0.817	0.813
RSD[3]	10.7	14.8	8.94	11.3
u*[4]	0.627	0.756	0.937	1.111[5]T
SI*[4]	73.8	111.8	107.0	136.7[5]

[1]SI is g/$A^{0.73}$ d and u is degree of maturity in BW (u = BW/A), where A is mature BW (kg). The breed-sex combinations were both sexes of Suffolk and Scottish Blackface sheep, and their cross.

[2]Feeds: high quality (H) protein content; low energy (LE) content; ryegrass (RG); and Lucerne (LUC). All feeds were pelleted.

[3]RSD = residual SD.

[4]The maximum scaled intake (SI*, g/$A^{0.73}$ d), and the degree of maturity (u*) at which this occurred.

[5]As u cannot exceed 1, the SI at u = 1 was calculated as 135.4 g/$A^{0.73}$ d.

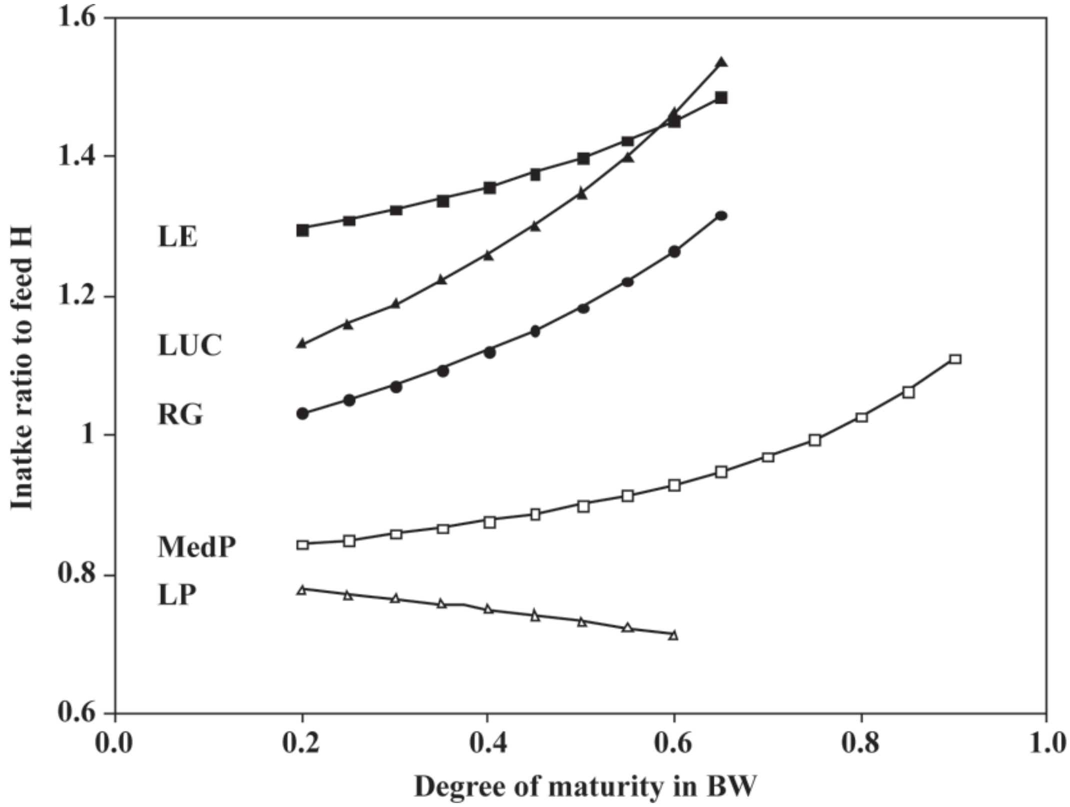

Figure 6. The calculated ratios of scaled intake (g/$A^{0.73}$ d, where A is mature weight in kg) to that on the high quality feed (H) of 5 limiting feeds plotted against degree of maturity in BW. The 5 diets were Lucerne (LUC; ▲), low energy content (LE; ■), ryegrass (RG; ●), medium protein content (MedP; □), and low protein content (LP; Δ), which are described in Table 1.

is therefore not sensible to expect intake expressed as I/BW^z to be constant as BW increases as the animal grows. Despite this, the practice of reporting intakes in this form is close to universal. The data on actual intake presented here show that over virtually no part of the range in BW for a given animal does intake of any of the feeds used here vary proportionally to $BW^{0.75}$. We can draw this conclusion from our data only because we present the actual intakes and not I/$BW^{0.75}$.

There were residual differences in SI between lines within the Suffolk breed, with the selected line eating more. Males also ate more than females. Both of these differences may reflect, at least in part, differences in fatness at a degree of maturity as Tolkamp et al. (2006) found that intake per unit BW increased as fat content decreased for a given breed. The observed differences between breeds and sexes in SI may also reflect differences in fatness. Furthermore, given the difficulty of accurately estimating mature size for a given kind of sheep (in particular the Scottish Blackface and the reciprocal cross), our apparent breed type differences may merely be the result of poor estimation of the genetic size parameter A.

Feed Composition

The value of SI* varied with feed composition. Feeds vary in many dimensions, some of which are believed to be relevant to intake, and our range of limiting feeds (low and medium protein contents, LE, RG, and LUC) was not comprehensive. However, the data from these feeds could be used to test whether SI relative to that on H varied with u in a similar way, or not.

It is possible that the observed intakes reflect the capacity of these sheep to deal with 1 or more constraints present in these feeds. Across a range of feeds that limited the growth rate of swine, it was found that none of the commonly accepted measures of the extent to which a feed might constrain intake (DE content, indigestibility of the OM, and NDF) could account for the observed intakes (Kyriazakis and Emmans, 1995). However, intake was closely related to the water holding capacity of the feeds used, which was confirmed by Tsaras et al. (1998) for a wider range of feeds. The results in Table 9 indicate that neither indigestible OM nor NDF could account for the differences that were observed in sheep in the present study. It may be that there is a measure of feeds for ruminants analogous to water holding capacity for swine, but we have not found it.

In the Appendix, it is shown that the quadratic model with no intercept in its usual form can be reparameterized in terms of SI_m, the SI at maturity, and u*. Across our 6 feeds, it happened that the value of u* increased as SI_m increased, the regression was u* = 0.422 + 0.0047 SI_m (r 0.88). This empirical relationship

Table 9. Scaled intakes (SI; g/$A^{0.73}$ d), ME (SMEI; kJ/$A^{0.73}$ d), indigestible OM (SIOMI; g/$A^{0.73}$ d), and NDF (SNDFI; g/$A^{0.73}$ d) at 2 degrees of maturity in BW (0.3 and 0.6) for 2 categories of animals and 6 feeds[1]

	0.3 maturity				0.6 maturity			
Breed and diet	SI	SMEI	SIOMI	SNDFI	SI	SMEI	SIOMI	SNDFI
Suffolk, males only								
H	58.8	616	5.4	12.7	81.9	857	7.5	17.7
MedP	50.4	547	3.2	10.1	76.1	825	4.8	15.3
LP	42.2	463	2.4	7.9	66.6	731	3.8	12.4
Mixed breeds, both sexes								
H	51.3	537	4.7	11.1	72.0	754	6.6	15.5
LE	69.1	411	30.8	38.0	104.7	622	46.7	57.5
RG	55.7	510	12.7	26.3	91.0	833	20.8	43.0
LUC	61.4	481	18.5	25.9	106.4	835	32.1	44.9

[1]A is mature size (kg). Categories are male Suffolk selection and control line sheep or both sexes of Suffolk and Scottish Blackface sheep and their cross (mixed breeds). Feed: high quality (H), medium (MedP), and low (LP) protein content; low energy (LE) content; ryegrass (RG); and Lucerne (LUC). All feeds were pelleted.

could be approximated by $u^* = 0.5 + 0.004\ SI_m$, which recognizes that the value of u* must exceed 0.5 for there to be a maximum. As the range of feeds used was necessarily restricted, we do not want to claim more for this relationship than that it gave a reasonably good description of our data. However, it would be useful to estimate the relationship between u* and SI_m across a wider range of feeds. The value of SI_m for a particular feed would be expected to reflect its ME content and the efficiency with which its ME is used for maintenance (Agricultural and Food Research Council, 1993).

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APPENDIX

When equations describing protein growth and fattening were combined with the genetic size-scaling rules of Taylor (1980), and the energy system of Emmans (1994), it was possible to predict the relationship between the scaled intake, as energy, and the degree of maturity in body protein. The function was not simple. Lewis and Emmans (2007) predicted weights of water and ash from the weight of protein in sheep. By combining the estimates of intake with those for BW, it was possible to plot scaled feed intake, SI g/$A^{0.73}$ d, against the degree of maturity in BW, u = BW/A.

Using parameter values likely to apply to growing sheep (Emmans, 1997), graphs of SI against u were created to examine to what extent they might be approximated by some simple form of function. As shown in Figure 7, the fit of a quadratic form with zero intercept, while not perfect, was very close: R^2 values of 0.992 and 0.999 for the 2 cases shown.

The quadratic equation is

$$SI = (a \times u) + (b \times u^2) \quad [A1]$$

when u = 1, SI = SI_m, which is the scaled intake at maturity. The equation becomes

$$SI_m = a + b. \quad [A2]$$

Equation A1 can be differentiated to give

$$dSI/du = a + (2b \times u) \quad [A3]$$

when SI is at its maximum value, dSI/du = 0 and u = u*, the degree of maturity at which this maximum intake occurs. The 2 conditions of A2 and A3 can then be combined to produce the equation relating SI to u, with SI_m and u* as the parameters instead of a and b, as in A1. The equation is

$$SI = (SI_m \times \{1 - [1/(1 - 2u^*)]\}) \times u + [SI_m/(1 - 2u^*)] \times u^2. \quad [A4]$$

The parameters SI_m and u* are biologically more easily understood than the parameters, a and b, used in formal Eq. A1.

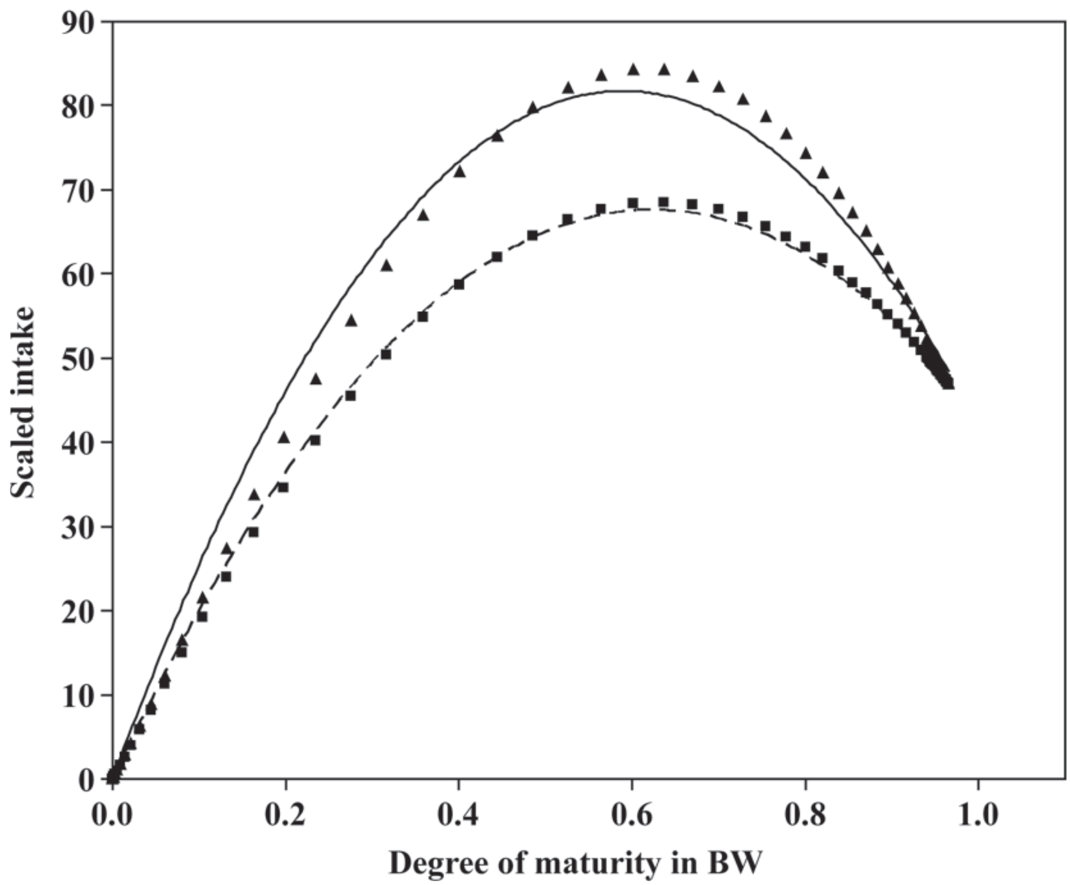

Figure 7. Predicted scaled intake (g/$A^{0.73}$ d, where A is mature weight in kg) plotted against degree of maturity in BW, u = BW/A. For (▲), the mature ratio of lipid to protein is 4.5, and the Gompertz rate parameter interspecies mean value is 0.02335; for (■), the ratio is 2.0 and value of the rate parameter has been multiplied by 1.3. For both, the quadratic equations have been fitted through the origin.