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The effect of subclinical intestinal nematode infection on the diet selection of growing sheep

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(*Received 2 August 1993 – Revised 1 February 1994 – Accepted 2 March 1994*)

To test the hypothesis that subclinical gastrointestinal parasitism, associated with an impairment in N digestion and metabolism and a reduction in the voluntary feed intake (VFI), could affect the diet selection of sheep given a choice between two feeds that differed in their crude protein (CP) content, twenty-four Texel × Scottish Blackface ewe lambs growing from 28 to 48 kg live weight (LWT) were given a daily dose of 2500 larvae of the intestinal nematode *Trichostrongylus colubriformis*; twenty-four similar lambs were used as uninfected controls. Six infected and six control lambs were given a free choice between two pelleted feeds (10·4 MJ metabolizable energy/kg), with different CP contents (90 (L) and 214 (H) g CP/kg fresh feed respectively). In addition, eighteen parasitized and eighteen control sheep were given access *ad lib.* to either feed L, or feed H, or their mixture M (164 g CP/kg; twelve per feed), in order to quantify the effects of the feeds when offered alone, and to test for any interactions between feed CP content and parasitism on the performance of the lambs. Intestinal parasitism reduced significantly ($P < 0.001$) both the rates of LWT gain (by 30%) and VFI (by 10%). The adult and developing parasitic forms took 4 weeks to establish and develop to a significant adult worm population (as judged by the faecal egg counts and blood variables) and until then there was no effect of parasitism on the performance of the lambs. The diet selection of the lambs given a choice between two feeds was similar between the two groups in the first 4 weeks of the experiment, but differed significantly ($P < 0.05$) in the second part of the experiment (4th week to the end). Thus, while parasitized lambs had a reduced rate of feed intake, by changing their diet selection they achieved a daily rate of CP intake similar to the control ones. However, since the parasitized lambs had a reduced rate of LWT gain, they also consumed a higher total amount of CP to reach the same LWT. It is concluded that sheep infected daily with a small number of larvae of *T. colubriformis* and given a choice between two feeds that differ in their protein contents are able to modify their diet selection in order to meet the increased protein requirements resulting from such an infection.

Appetite: Intestinal nematode infection: Protein intake: *Trichostrongylus colubriformis*

The theory of nutritional wisdom suggests that an animal senses its internal state (i.e. nutritional demands) by some means, and subsequently makes dietary choices between available and appropriate feeds, which enable it to satisfy these particular demands (Kyriazakis, 1989; Kyriazakis & Emmans, 1991). Any changes in the physiological state of the animal that have an effect on its requirements can be expected to be manifested in appropriate choices. There is now clear evidence (Hou *et al.* 1991; Kyriazakis & Oldham, 1993) to show that sheep are able to select a diet that meets their requirements for fast growth and avoid excess of protein intake when they are given a choice between two feeds that differ in their protein:energy ratios. An important question then is, would an increase in the protein requirements, in relation to energy, of sheep, lead to a change in their diet selection in order to increase the protein content of the diet?

Subclinical gastrointestinal parasitism in growing sheep is associated with an impairment in protein metabolism. Adult and developing worms cause damage to the gastrointestinal mucosa that results in increased plasma leakage and therefore endogenous protein loss into the lumen (Steel *et al.* 1980; Poppi *et al.* 1986, 1990); at later stages of the infection, protein is directed towards repair and replacement of the damaged mucosa and the invocation of the immune response (Kimambo *et al.* 1988). These changes result in an increase in the protein requirements of the parasitized animal and the need for a higher dietary content is accentuated by the reduction in the voluntary feed intake that accompanies such parasitism (Symons, 1985).

The objective of this experiment was to test whether young growing sheep infected daily with a number of the small-intestinal nematode *Trichostrongylus colubriformis* ('trickle infection') at a similar level to that encountered when they are grazing on a moderately contaminated pasture, are able to modify their diet selection when they are given access to two feeds that differ in their protein contents, in order to meet their increased protein requirements resulting from such an infection. In addition, animals given access to a series of single feeds with different protein contents were used to test for any interactions between the feed protein content and the development of the subclinical parasitism in growing lambs.

MATERIALS AND METHODS

Animals and housing

Forty-eight Texel × Scottish Blackface ewe lambs were weaned at 6–8 weeks of age (on 8 June 1992) and moved to the individual pens of the experimental unit. Before weaning the lambs were maintained with their mothers on a 'clean' pasture which carried no larvae of *T. colubriformis*. The lambs had a mean live weight of 15·1 (SD 1·51) kg and were given a live-weight-based allowance (3·5% of their live weight) of a high-quality feed with 180 g crude protein (nitrogen × 6·25; CP) and 10·4 MJ metabolizable energy (ME)/kg fresh feed. This allowance was estimated to be just below their *ad lib.* feed intake, thus ensuring that all lambs would reach the initial experimental live weight with a similar gut-fill. Faecal samples were taken from ten lambs, selected at random, on entering the experimental unit and then all lambs received an oral dose of the anthelmintic Oramec (Ivermectin, 200 pg/kg body weight; MSD AGVET, Hoddesdon, Herts.). Screening of the faeces of the ten lambs showed that they were free from any nematode eggs.

The experimental unit was a concrete-floored animal shed that was naturally ventilated, and had six rows, each of eight adjustable pens. Each pen measured 1·50 × 1·87 m and its slatted floor was raised 0·35 m above the concrete. Either one or two (according to experimental treatment) food troughs and a water bowl which gave free access to water were located in each pen. The pens with two troughs were chosen randomly within the shed.

Feeds

Two basal feeds with different CP concentrations (low (L) and high (H)), but with the same calculated ME concentration, were formulated and made into pellets (Table 1). The low-protein feed was formulated to be inadequate in CP to support potential growth when offered on an *ad lib.* basis (Agricultural Research Council (ARC), 1980); the protein content of feed H was intended to be above the requirements of the lambs. Both feeds were intended to be non-limiting in minerals and vitamins. In addition, a mixture of feeds L and

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Table 1. *Ingredients and chemical compositions of the experimental feeds (g/kg fresh weight)*

	Feed		
	L	M	H
Ingredients			
Barley	378·8	348·6	328·1
Oatfeed	49·5	69·1	82·1
Unmolassed sugar-beet pulp	478·8	292·4	168·1
Hipro soya	—	197·7	329·4
Molasses (CMS 20)*	70·0	70·0	70·0
Salt	6·5	7·7	8·5
Dicalcium phosphate	9·6	3·8	—
Limestone flour	4·2	8·7	11·8
Vitamin + mineral mix	2·0	2·0	2·0
Calcined magnesite	0·5	—	—
Component			
Dry matter	877	869	874
Crude protein	90	164	214
Ash	65	66	68
Crude fibre	127	103	85
ADF	152	127	106
NDF	297	268	243
Ether extract	20	20	22
Gross energy (MJ/kg)	14·89	15·31	15·67
Metabolizable energy (MJ/kg)†	10·4	10·4	10·4
Ca	10·0	9·0	8·3
P	3·2	3·3	3·6
Mg	1·4	1·5	1·8
Na	2·7	2·2	4·2
K	6·2	8·7	11·9
S	3·2	3·0	3·2
Cu (μmol/kg)	148	155	177
Mo (μmol/kg)	0·91	1·65	1·94

L, low-protein feed; M, mixture of low- and high-protein feeds (2:3 w/w); H, high-protein feed; ADF, acid-detergent fibre; NDF, neutral-detergent fibre.

* CMS 20, condensed molasses solubles blended with 20% cane molasses (Intermol, Knowle Park, Cobham, Surrey).

† Calculated from food tables.

H (2:3; w/w), food M, was also made and pelleted; this was intended to be close to the requirements of the animals (ARC, 1980).

Design

Period 1. As each lamb reached 20 kg live weight it was allocated to one of four treatments (*n* 12 per treatment): free and continuous access to the single feed L, M or H, or a free and continuous choice between feeds L and H (treatment L/H). The lambs were allocated randomly to the treatments taking account of age at 20 kg live weight. This period ended when each lamb reached 28 kg live weight.

At the start of this period the lambs that were to be offered a choice between two feeds were given the opportunity to experience both of the feeds which were subsequently to be given as a choice. Each of the two feeds was offered alone on alternate periods of 2 d (four times), and subsequently on alternate days (once); thus, the experience period lasted for

10 d in total. This training period was a slight modification of the method described by Kyriazakis & Oldham (1993). The position of the two feeds was not changed throughout the experiment, but it was randomized across lambs.

Period 1 allowed lambs given a choice between two feeds to establish their diet selection before they were challenged with parasites in Period 2.

Period 2. At 28 kg live weight half of the animals within each treatment were given orally a daily dose of 2500 L_3 larvae of *Trichostrongylus colubriformis* suspended in 10 ml water. The remaining animals were used as uninfected controls. This part of the experiment ended when each lamb reached 48 kg live weight.

Management and measurements taken

During the first week of the experiment (i.e. the experience period), as the lambs were changed from controlled feeding to the experimental feeds, they were given 800, 800, 800, 1000, 1000, 1200 and 1200 g/d respectively in two separate allowances, before they were given access *ad lib.* to the feed.

The lambs were weighed once a week during the morning up to 26 or 46 kg live weight, and then daily until they reached the target weights of 28 or 48 kg, for Periods 1 and 2 respectively. They were offered feed twice daily (morning and afternoon) to minimize spillage. Feed refusals were weighed daily and discarded. For the choice-fed animals, both troughs were removed at the same time, fresh feed was then placed in the troughs after weighing the refusals. An effort was made to offer each lamb similar quantities of feeds at the start of the day and to ensure that the amount of feed offered was at least 1·25 times their *ad lib.* feed intake.

Faecal egg counts were monitored weekly, by taking a rectal faecal sample from each infected lamb, and the number of eggs/g (EPG) of fresh faeces was estimated by using a modification of the flotation method described by Christie & Jackson (1982). One tenth, one fifth or all of the eggs recoverable from 1 g of faeces were counted, following centrifugal flotation in saturated NaCl in a collapsible cellulose acetate tube. Blood samples were taken weekly by jugular venepuncture during the morning before feeding and were allowed to settle in a cool place before being centrifuged the following morning for 20 min at 2500 ***g***. The resulting serum was stored at $-20°$ until it was analysed. The levels of albumin, total protein ($N \times 6{\cdot}25$), Ca, P and urea were subsequently determined in the serum by the use of a Monarch 2000 microcentrifugal analyser (Instrument Laboratory, Warrington, Ches.) using standard commercial kits. Serum globulin was calculated by difference.

The lambs received a minimum of 16 h light/d and the ambient temperature ranged from a mean daily minimum of 11·1 (SD 3·3) to a mean daily maximum of 15·1 (SD 3·3)°.

Statistical analysis

The results from Period 1 were analysed by an analysis of variance with feeding treatment as factor. The results from Period 2 were analysed by an analysis of variance with feeding treatment and parasitism as factors. For the diet selection data, those of Period 1 were used as a covariate for the analysis of Period 2.

RESULTS

Period 1

The daily rates of live-weight gain, feed intake and feed conversion efficiency (FCE) of all lambs during Period 1 are shown in Table 2. None of these measurements was affected by the age at which sheep reached the initial experimental weight (20 kg). The daily feed intakes are given on a fresh-weight basis, since the dry matter content of all feeds was high

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Table 2. *The performance of sheep given access either to feeds with different protein contents or a choice between two such feeds, from 20 to 28 kg live weight*†

(Mean values for twelve sheep per dietary group)

Feed	CP content (g/kg)	Days	Live-weight gain (g/d)	Feed intake (g/d)	FCE (g gain/ g food)	Prop H selected (g/kg TFI)
L	90	39·1	217	790	0·275	—
M	164	19·9	420	1178	0·357	—
H	214	20·8	407	1143	0·358	—
L/H	174‡	20·3	417	1130	0·369	677
SED		2·05	24·8	34·1	0·021	28·1§
Significance of:						
Feed		***	***	***	***	—

CP, crude protein (N × 6·25); FCE, feed conversion efficiency; Prop H, proportion of feed H selected; TFI, total feed intake; L, low-protein feed; M, mixture of low- and high-protein feeds (2:3; w/w); H, high-protein feed; L/H, low- and high-protein feeds offered simultaneously; SED, standard error of the difference between means. *** $P < 0·001$.

† For details of diets and procedures, see Table 1 and pp. 666–668.

‡ Selected.

§ Standard error of the mean.

and did not differ between feeds. Animals on the low-protein feed (L) grew and ate feed at a slower rate ($P < 0·001$), and converted feed less efficiently ($P < 0·001$) than lambs on any other treatment. As a consequence they took almost twice as long to reach 28 kg live weight.

The lambs given a choice between the two feeds L and H selected a diet that consisted of 677 (SE 28) g feed H/kg total feed intake (TFI) and had a CP concentration of 174 (SE 3·5) g CP/kg feed. The proportion of feed H chosen was statistically different from random selection (i.e. different from proportion of feed H = 500 g feed H/kg TFI). Their performance was similar to those given access either to feed M or H.

Period 2: clinical observations

Screening of the faeces at the beginning of Period 1 showed that all animals used in the experiment were free from nematode eggs. During the dosing period (Period 2) all lambs in the infected groups showed an erratic pattern of excretion of soft faeces, starting from the sixth week of this period. Nematode eggs in the faeces of the infected lambs for the period of dosing are shown in Fig. 1. Appreciable numbers of eggs started to appear in the faeces by week 4 and mean EPG were maximal by the fifth week of dosing. The EPG had declined to small numbers by the end of the experiment indicating the development of immunity. There were no differences between the four feeding treatments in the pattern of the concentrations of eggs in the faeces. Uninfected controls remained free from any nematode eggs in their faeces throughout Period 2.

The mean values for the serum variables in weeks 1–4 and 5–8 of Period 2 for both infected and uninfected lambs are shown in Table 3. During the first 4 weeks of the dosing period there were no differences in the levels of Ca, total protein, globulin and albumin in the serum between the infected and control lambs. The only exception was the level of P in the serum of the infected lambs that started to decline from the third week of dosing ($P < 0·001$). Feeding treatment affected significantly only the level of P in the serum, during this sub-period.

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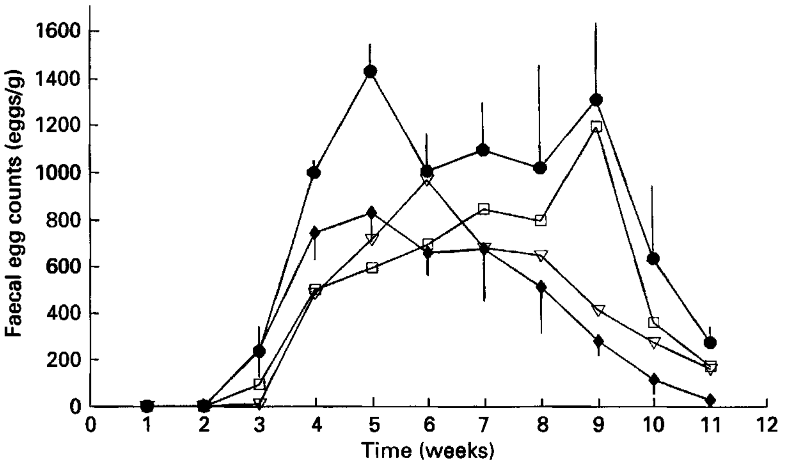

Fig. 1. Mean weekly faecal egg counts (eggs/g faeces) of sheep infected daily with 2500 *Trichostrongylus colubriformis* larvae and given access to feeds with low (□), medium (◆) or high (●) protein contents, or a choice between two feeds with low and high protein contents (▽). Values are means for six sheep, with their standard errors indicated by vertical bars (extreme values only). For details of diets and procedures see Table 1 and pp. 666–668.

During weeks 5–8 of Period 2 there were significant differences between infected and control lambs in the level of the variables measured in the serum. Infected lambs had significantly higher levels of Ca and globulin, and significantly lower levels of P and albumin in their serum than uninfected controls. Feeding treatment also had an effect on the levels of Ca in the serum. This was due to the significantly higher levels of Ca in the serum of the lambs given access to feed L.

The levels of urea in the serum did not change significantly throughout the experiment and were not affected by dosing. The only effect was due to feeding treatment, with animals on feed L and feed H having the lowest and highest concentrations of urea respectively (the grand means for the whole period were: 1·94, 9·15, 12·24 and 8·42 g/l for treatments L, M, H and L/H respectively).

Period 2: growth and feed intake

The daily rates of live-weight gain and feed intake, and FCE of all animals are shown in Table 4. Dosing affected significantly the live-weight gain of the animals, but this was to the same extent across all of the treatments. Uninfected lambs on treatments M, H and L/H took an average of 71·4 (SE 1·89) d to reach 48 kg live weight, whereas infected animals took an average of 96·5 (SE 3·99) d to reach the same live weight. Due to the poor live-weight gain of sheep given access to feed L and the limited availability of infective larvae, these animals could only be kept on the experiment for a period of 91 d. At this stage their live weights were 45·7 (SE 0·67) and 41·5 (SE 1·04) kg, for the uninfected and infected animals respectively ($P < 0{\cdot}001$).

Infected animals developed an inappetence at around the third to fourth week after the onset of larval infection (see Fig. 2 for the feed intake of L/H sheep). Their average rate of feed intake did not increase any further beyond this point, but remained at 1500 g/d for the M, H, L/H and 1300 g/d for the L animals. The extent of inappetence was variable between individual animals, but was not affected significantly by feeding treatment. Two animals, one on feed L and one on feed M, developed a severe anorexia in the later stages of the experiment (their feed intake declined below 400 g/d) and had to be removed from

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Table 3. *The effect of intestinal parasitism with* Trichostrongylus colubriformis *on the concentrations of serum constituents of sheep given access either to feeds with different protein contents or a choice between two feeds with low and high protein contents*†

(Mean values for six sheep per feeding treatment)

Feeding treatment	Parasitism	Ca (mmol/l) 1–4 weeks	Ca (mmol/l) 5–8 weeks	P (mmol/l) 1–4 weeks	P (mmol/l) 5–8 weeks	Total protein (g/l) 1–4 weeks	Total protein (g/l) 5–8 weeks	Globulin (g/l) 1–4 weeks	Globulin (g/l) 5–8 weeks	Albumin (g/l) 1–4 weeks	Albumin (g/l) 5–8 weeks
L	–	2·61	2·70	2·56	2·58	57·3	57·3	31·0	30·9	26·2	26·5
	+	2·68	2·79	2·19	1·96	56·6	59·3	30·1	34·1	26·5	25·1
M	–	2·69	2·62	2·82	2·55	58·2	59·7	31·0	31·8	27·2	27·8
	+	2·68	2·75	2·53	1·61	57·0	60·2	30·0	34·8	27·1	25·4
H	–	2·68	2·62	2·78	2·49	58·9	60·3	30·7	32·0	28·2	28·4
	+	2·63	2·70	2·44	1·95	58·9	61·7	31·3	34·8	27·7	26·9
L/H	–	2·65	2·58	2·81	2·51	57·0	58·1	30·8	31·4	26·2	26·7
	+	2·70	2·66	2·61	1·94	57·2	59·2	30·1	33·0	27·1	26·1
SED		0·056	0·051	0·143	0·189	1·88	2·08	1·47	1·92	0·76	1·03
Feeding treatment (F)		NS	**	**	NS	NS	NS	NS	NS	NS	NS
Parasitism (P)		NS	***	***	***	NS	NS	NS	**	NS	**
F × P		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

L, low-protein feed; M, mixture of low- and high-protein feeds (2:3; w/w); H, high-protein feed; L/H, low- and high-protein feeds given simultaneously; SED, standard error of the difference between means; NS, not significant.

** $P < 0.01$; *** $P < 0.001$.

† For details of diets and procedures, see Table 1 and pp. 666–668.

Table 4. *The effect of intestinal parasitism with* Trichostrongylus colubriformis *on the daily rates of live-weight gain, feed intake and feed conversion efficiency (FCE) of sheep given access either to feeds with different protein contents or a choice between two such feeds*†

(Mean values for six sheep per feeding treatment)

Feeding treatment	Parasitism	Growth rate (g/d)	Feed intake (g/d)	FCE (g gain/g feed)
L	–	201	1403	0·142
	+	142	1262	0·112
M	–	284	1669	0·171
	+	207	1523	0·134
H	–	275	1646	0·168
	+	212	1478	0·143
L/H	–	288	1663	0·173
	+	218	1485	0·146
SED		21·8	90·3	0·009
Feeding treatment (F)		***	***	***
Parasitism (P)		***	**	***
F×P		NS	NS	NS

L, low-protein feed; M, mixture of low- and high-protein feeds (2:3, w/w); H, high-protein feed; L/H, low- and high-protein feeds offered simultaneously; SED, standard error of the difference between means; NS, not significant.

** $P < 0·01$; *** $P < 0·001$.

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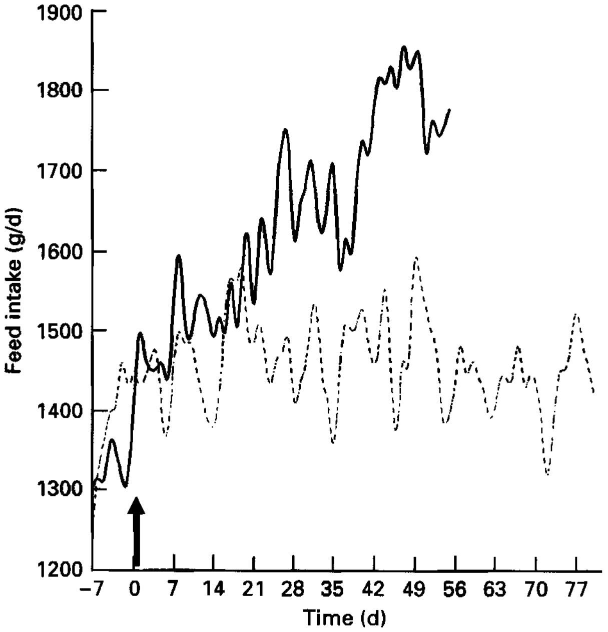

Fig. 2. The daily rate of total feed intake (g/d) of sheep infected with *Trichostrongylus colubriformis* (––––) and controls (——) given access to two feeds, one with a low protein content and one with a high protein content, as a choice. The arrow indicates the start of dosing with *T. colubriformis* larvae. For details of diets and procedures, see Table 1 and pp. 666–668.

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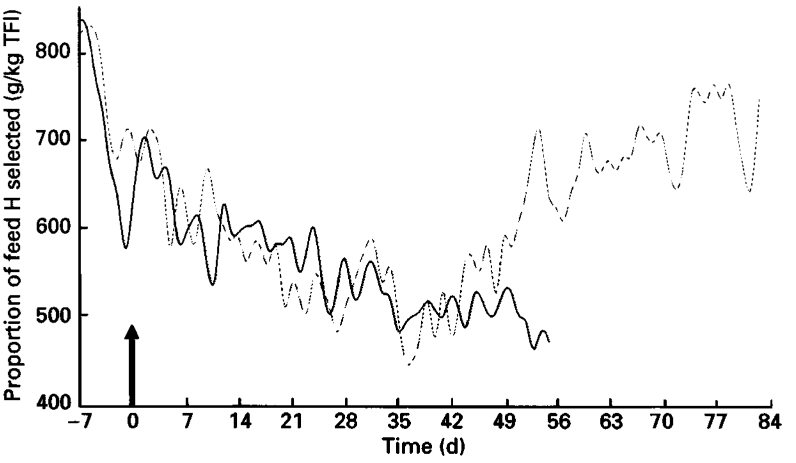

Fig. 3. The average daily proportion of the high-crude-protein feed (feed H) selected (g/kg total feed intake (TFI)) by sheep infected with *Trichostrongylus colubriformis* (----) and controls (——) given access to two feeds, one with a low protein content and one with a high protein content, as a choice. The arrow indicates the start of dosing with *T. colubriformis* larvae. For details of diets and procedures, see Table 1 and pp. 666–668.

the experiment, due to concerns about their welfare, on weeks 12 and 11 of Period 2 respectively. The feed intake of the uninfected lambs continued to increase with time and increasing live weight throughout the experiment.

Dosing affected adversely the FCE of the infected lambs, irrespective of feeding treatment. Sheep given access to feed L were less efficient feed converters than lambs on any other feeding treatment. The interaction between dosing and feeding treatment was not significant.

Period 2: diet selection

The proportion of feed H (prop H; g feed H/kg TFI) selected over time by the lambs given access to feeds L and H as a choice is shown in Fig. 3. The prop H selected declined systematically for the first 4 weeks of Period 2 for both infected and control lambs. Subsequently the prop H selected by the infected lambs started to increase, until it reached a maximum of 800 g feed/kg TFI on the eighth week of dosing and remained at this level for the remaining part of the experiment. Consequently, the average prop H selected for the first 4 weeks of Period 2 (or during the live weight interval 28–36 kg) was similar between the two groups (598 *v.* 594 (SED 121) g feed H/kg TFI), but significantly different for the remaining part of Period 2 (475 *v.* 622 (SED 64) g feed H/kg TFI, $P < 0{\cdot}05$) for the control and infected lambs respectively. Thus, the selected diets for these two sub-periods had an average CP concentration of 164 *v.* 164 (SED 14·9) and 149 *v.* 167 (SED 7·9, $P < 0{\cdot}05$) for the control and parasitized lambs respectively.

This mode of diet selection, together with the inappetence shown by the infected lambs, resulted in similar average daily intakes of protein consumed by both groups in both sub-periods of Period 2. The average daily intake of CP throughout Period 2 was 254 *v.* 245 (SED 21·5) g/d for the control and infected lambs respectively.

DISCUSSION

The clinical signs seen during the development of the infection in this experiment generally concur with previous observations on experimental subclinical infection with *T. colubriformis* (e.g. Coop *et al.* 1976; Kimambo *et al.* 1988; Poppi *et al.* 1990). Infected

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animals started to show moderate levels of eggs in their faeces by week 4 of dosing, indicative of a significant adult worm population with associated damage to the small intestine. The numbers of eggs in the faeces had declined by week 11 from dosing, which suggests that by then there was the start of a development of immunity by the lambs, so that fewer of the infective larvae were able to establish and/or there was an inhibition of egg production by the adult worms (Chiejina & Sewell, 1974).

Other clinical signs shown by the infected lambs were lower levels of P and albumin, and higher levels of Ca and globulin in their serum. The lower levels of albumin in the blood are the result of increased enteric loss of plasma into the gastrointestinal lumen (Steel *et al.* 1980; Poppi *et al.* 1986), and the lower levels of P the result of an impairment of P absorption (Poppi *et al.* 1985). Since the latter is not accompanied by any changes in Ca absorption, this results in high levels of Ca in the serum due to the lower rates of deposition of both macrominerals. The increase in globulin levels that continued throughout the experiment probably reflects an increased rate of immunoglobulin synthesis, associated with the development of immunity. All these differences in serum constituents between control and infected lambs became evident at the same time as the rise in the faecal egg counts and by inference the damage to the intestinal mucosa; the sole exception was the level of P in the serum which started to decline at an earlier stage.

The clinical symptoms listed above were manifested to the same extent in all feeding treatments, and in no case was there a significant interaction between level of protein in the feed and dosing. This is in agreement with the findings of Bown *et al.* (1991) who reported no difference in the development of subclinical infection and plasma albumin concentrations between protein-supplemented and unsupplemented lambs dosed with *T. colubriformis*. However, there is evidence in the literature (Abbott *et al.* 1988) that the protein level of the feed plays a role in the development and enhancement of the resistance to parasitic infection. In Abbott's experiment sheep dosed with a trickle infection of *Haemonchus contortus* and given access to a high-protein food (with 169 g CP/kg dry matter) developed resistance to infection after 17 weeks (as indicated by lower faecal egg counts and lower worm burdens), in contrast to a low-protein group (with 88 g CP/kg dry matter) in which no resistance appeared to develop. This finding with an abomasal nematode contradicts our results which show that the patterns of the faecal egg counts were similar between the two extreme protein foods L and H; in our case the faecal egg counts are taken as the sole indicator of the immune status of the lambs. This disagreement between our results and those of Abbott *et al.* (1988) is intriguing and perhaps points to a dietary factor other than protein being involved in the development and enhancement of immunity. One candidate might be a dietary mineral. In Abbott's experiment there was a reduction in feed intake with parasitism, but the degree of reduction is not known. Calculation of P intakes for the two feeds used (P. H. Holmes, personal communication) suggests that P intake may have been marginal in relation to requirements for the lower protein feed and there is evidence (Coop & Field, 1983) that such a limitation may have inhibited the development of resistance to infection. However, at this stage, one can only speculate on this possibility, though it would merit further effort.

The most significant effect of gastrointestinal parasitism on the host is the depression in voluntary feed intake. Large acute infections result in a very significant decrease in the rate of feed intake of parasitized lambs (Sykes, 1987), but a degree of inappetence is present even in subclinical infections. In the latter case the degree of inappetence reported in the literature varies between 6 and 30% (Poppi *et al.* 1990), and this variation has been attributed to different nutrient contents (most notably those of protein and P) of the feeds offered to parasitized lambs. It has also been suggested that this depression in feed intake is a direct result of the slower growth of the parasitized lambs, and that when feed intake

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is expressed per unit body weight, such a depression is no longer evident (Sykes, 1983). The results of the present experiment clearly show that there was a depression of the order of 10% in the feed intake of parasitized lambs growing from 28 to 48 kg live weight, which is similar to that previously recorded for this level of *T. colubriformis* infection (Sykes & Coop, 1976); this depression was independent of feeding treatment (level of CP in the feed). Parasitized lambs did not increase the rate of feed intake beyond the fourth week from dosing, and the depression was present until the end of the experiment (11–12 weeks from dosing). Thus the depression in feed intake can be seen as the direct effect of dosing rather than an indirect effect of slower growth. The feed intake of parasitized animals is expected to increase once a high level of host immunity has been developed; our results suggest that such immunity had not yet been fully developed by the lambs by the end of the experiment and concur with the results of Kimambo *et al.* (1988).

The diet selection of both parasitized and control lambs changed systematically during Period 1 and the first 4 weeks of Period 2: the proportion of the high-protein feed selected declined systematically, and as a consequence the CP content of the selected diet also declined. This is in agreement with the expected decline in the CP requirements of the lambs in relation to energy as they grow. Such a decline in the CP content of the diet selected by growing animals has been repeatedly demonstrated in single-stomached animals (e.g. pigs, Kyriazakis *et al.* 1993), but it is only the second time that it has been shown to happen with growing sheep (the first being that of Cropper, 1987). This demonstration probably reflects the duration of this experiment and the formulation of feeds used.

Following this initial decline the parasitized animals started to increase the proportion of the higher protein feed in their diet. This change in their diet selection is assumed to reflect a state of enhanced protein requirements in these lambs, due to an increase in endogenous protein losses and a depression in their voluntary feed intake. The fact that there is almost a week-long interval between the depression in feed intake and the change in diet selection is not surprising in light of the relatively slow rates of digestion and passage of the feed in ruminant animals. Control sheep continued to show a small decline in the proportion of the high-protein feed selected in their diet, for the remaining part of Period 2, but since this was a weight-based experiment they remained on the experiment for an additional 4–5 weeks, whereas the parasitized animals remained for an additional 8–9 weeks. Therefore, any comparison in the diet selection between control and parasitized sheep for the second part of Period 2 is not absolutely legitimate, since we do not know how the control animals would have reacted if they had stayed on the experiment for an equal period of time. However, there is no biological reason to suggest that uninfected sheep would change their diet in a similar way to the parasitized ones, but with a time lag of approximately 4 weeks. During the whole of Period 2 the daily rate of CP intake for both parasitized and uninfected lambs was very similar (245 *v.* 254 (SED 21) g CP/d respectively). One way of seeing this result is that sheep responded to the parasitic challenge by adjusting their diet selection to the extent that daily rate of CP intake was maintained but not enhanced. This of course will not be advantageous to an animal with an enhanced protein requirement (this is likely to increase even further during the latter part of the infection, due to protein being directed towards the repair and replacement of the damaged tissue and the innovation of the immune response), and we suggest that the similarity in the daily CP intake between the two groups was rather fortuitous and the result of the experiment being a weight- rather than a time-based one.

The major constraint on the parasitized animals given access to feeds high in protein content (M or H) or a choice between two feeds that differed in CP content was the reduction in energy intake that was due to the depression in feed intake. For this reason parasitized lambs grew at a slower rate and took a longer time to reach 48 kg live weight.

There was no formal significant interaction between parasitism and feeding treatment on the growth of lambs, which suggested that parasitized animals were affected to the same extent, independently of feeding treatment. However, there was an indication that the ratio of the gain of parasitized:control animals was at its lowest (0·71) on feed L and at its highest on treatments H and L/H (0·77 and 0·76 respectively). Similarly, the FCE ratio of parasitized:control animals was 0·79, 0·86 and 0·85 respectively. It is interesting to consider whether an increase in the protein content of the feed would have had an effect on the body composition of parasitized sheep. Bown (1986) has shown that abomasal infusion of casein improved significantly the rate of protein retention of parasitized animals, whereas glucose infusion had an effect on total energy but not protein retention. These considerations suggest that sheep given a choice between two feeds that differ in their protein content but have similar energy content, such as the choice offered to the lambs in this experiment, might be able to increase the rate of protein retention to that of uninfected controls by modifying their diet selection.

In conclusion, this experiment is the first indication that sheep infected daily with a small number of larvae of the small-intestinal parasite *T. colubriformis* and given a choice between two feeds that differ in their protein content, modify their diet selection in order to meet the increased protein requirements resulting from such an infection. To our knowledge, this is the first demonstration for ruminant animals to suggest that any change in their physiological state that has an effect on their requirements will be manifested by appropriate changes in their diet selection.

This work was supported by an Agricultural and Food Research Council/BOCM Pauls cooperative research grant and by funding from the Scottish Office Agriculture and Fisheries Department. The expert technical assistance of D. H. Anderson, E. Jackson, T. McHale and J. Small, and the help of Dr M. Lewis with the formulation of the feeds are gratefully acknowledged.

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