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The patho-physiology of *Trypanosoma congolense* in Scottish Blackface sheep: influence of diet on digestive function

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Abstract

The influence of types of roughage, barley straw (diet B) versus *lucerne hay (diet L), on the patho-physiology of a* T. congolense *infection was compared in eight pairs of Scottish Blackface male twin lambs. One animal of each twin pair was infected and the other used as a pair-fed control. Voluntary food intake, body weight, digestive function, various blood haematological and biochemical measurements were made.*

Voluntary organic matter intake decreased significantly after the T. congolense *infection, the decrease being greater in the diet L group than in the diet B group lambs ($P < 0.01$). The apparent digestibility coefficients of crude protein and organic matter were significantly lower in the infected lambs ($P < 0.01$). Mean retention time of the roughage through the digestive tract in the animals given barley straw was significantly longer ($P < 0.05$) due to a lower rumen outflow rate constant ($P < 0.01$). Infection resulted in longer mean retention times ($P < 0.01$).*

Packed cell volume (PCV) was significantly lower before infection in the animals given diet B ($P < 0.01$). After infection, diet ($P < 0.01$) and infection ($P < 0.01$) had an additive effect on PCV. The anaemia was both macrocytic ($P < 0.05$) and hypochromic ($P < 0.01$).

Diet B resulted in higher plasma cholesterol ($P < 0.05$), but lower plasma urea ($P < 0.01$) and albumin ($P < 0.01$) concentrations before infection than diet L. The T. congolense *infection significantly lowered plasma cholesterol ($P < 0.01$) and increased plasma urea ($P < 0.01$) concentrations compared with the uninfected controls. Plasma albumin concentrations decreased, but were more affected by nutrition ($P < 0.01$) than by infection ($P < 0.05$).*

It was concluded that the patho-physiological effects of the T. congolense *infection in the Scottish Blackface lambs were affected by the type of roughage offered, but that these effects were additive rather than interactive to the effects of infection.*

Keywords: *digestion, roughage, sheep, trypanosomiasis.*

Introduction

Long-term monitoring studies in trypanotolerant N'dama cattle kept under village conditions in The Gambia have revealed that the effects of trypanosome infections are more severe during the dry season when the quality of the food available is lower (Agyemang *et al.*, 1990 and 1992). In a recent study, at the University of Glasgow Veterinary School, it was found that high protein diets can ameliorate the effects of *Trypanosoma congolense* infections in Scottish Blackface sheep (Katunguka-Rwakishaya *et al.*, 1993). Similar results have been demonstrated in ovine fascioliasis (Berry and Dargie, 1976) and haemonchosis (Abbott *et al.*, 1986). Whereas a number of experiments have been conducted on the effects of protein supplementation during parasite infections, no studies have been reported on the effects of different types of roughage. In a recent study in The Gambia it was found that N'dama heifers reduced their intake of poor quality *Andropogon guyanus* hay but consumed all the groundnut hay and cake offered after an infection with *T. congolense* (Romney *et al.*, 1994). In the present study the effects of diet on an infection with *T. congolense* were investigated in Scottish Blackface lambs offered diets based on barley straw and

Table 1 *Dry matter (DM; g/kg), organic matter (OM; g/kg), metabolizable energy (ME; MJ/kg), fermentable metabolizable energy (FME; MJ/kg), neutral-detergent fibre (NDF; g/kg), acid-detergent fibre (ADF; g/kg), ether extract (EE; g/kg), crude protein (CP; g/kg), effective rumen degradable dietary protein (ERDP) and digestible undegraded protein (DUP) of the diet components*

	Diet B		Diet L	
Diet composition	Concentrate	Barley straw	Concentrate	Lucerne hay
DM	862	873	862	894
OM	944	953	956	901
ME†	13·3	6·5	13·3	8·8
FME†	12·7	5·9	12·7	7·8
NDF	229	781	256	343
ADF	52	490	46	265
EE	14	9	12	15
CP	209	46	109	206
ERDP†	138	27	84	116
DUP†	71	8	18	47

† Values derived from *in-sacco* degradation.

lucerne hay. Barley straw, like *Andropogon guyanus* hay, is high in fibre but low in nitrogen, whereas lucerne hay is high in both fibre and nitrogen. The differences in quality of the two roughages resulted in different levels of energy being consumed on the two treatments. To reduce the difference in level of crude protein between the diets extra protein was added to the concentrate offered to the lambs receiving barley straw. Scottish Blackface lambs were used in this experiment since they are hardy animals and have been shown, like trypanotolerant breeds, to resist the effects of trypanosomiasis well. The infected and control animals were pair-fed to avoid confounding direct effects on nutrient utilization with decreased intake due to infection.

Material and methods

Animals, food and housing

Eight pairs of twin castrated Scottish Blackface lambs (aged 5 months) were selected from a local hill farm flock in the west of Scotland. Four extra lambs were slaughtered at the start of the experiment to use as baseline control animals.

Four pairs were offered chopped barley straw plus 425 g of a pelleted barley/soya-bean meal concentrate mixture (diet B) and the other four pairs chopped lucerne hay plus 425 g pelleted barley concentrate (diet L). The concentrates were offered in order to provide the lambs on diet B a diet slightly above their maintenance requirements. The roughage was offered *ad libitum* (proportionately 0·20 greater than previous day's intake) to one animal of each pair (I). The other animal of each pair was used as a pair-fed control (PC), being offered the same amount of food as the infected counterpart had consumed on the previous day. The roughage and concentrate foods were individually characterized by the measurements of the rates of degradation following suspension in a polyester bag in the rumen of fistulated cows. The measurements were performed in duplicate. The concentrate foods were examined after 0, 8, 16, 24 and 48 h and the roughages after 0, 16, 24, 48 and 72 h as proposed by Ørskov and Mehrez (1977). The data obtained were fitted to an exponential function: $y = a + b(1 - e^{-ct})$ as described by McDonald (1981) using a program supplied by Chen ('Neway', Rowett Research Institute, personal communication). The results are shown in Table 1. Prior to infection, intake of diet B resulted in metabolizable protein (MP) and metabolizable energy (ME) intakes of approximately 70 g/day and 8·3 MJ/day, for diet L MP and ME intakes were approximately 140 g/day and 13·3 MJ/day. The animals were given food twice a day at 09.00 and 15.00. The lambs had free access to fresh water at all times and were housed in individual pens on a concrete floor bedded with wood shavings.

Infection

Three weeks after the experiment started the lambs in group I were infected with *T. congolense* 1180 (GRVPS 57/6) isolated in Serengeti, Tanzania (Nantulya *et al.*, 1984). The trypanosomes were obtained from irradiated mice during the first rising parasitaemia. Each animal was inoculated intravenously with 5×10^5 trypanosomes in 3 to 4 ml phosphate buffered saline (PBS) (containing 1·5% glucose).

Measurements

Individual food intakes were recorded daily by collecting refusals between 8.00 and 9.00 h. The animals were weighed once a week.

Organic matter (OM) and crude protein (CP) apparent digestibilities of the food were measured during three periods of 7 days each, one before and two after infection. Period 1 lasted from day −10 to day −3 before infection, period 2 from day 19 to day 26 after infection and period 3 from day 50 to 57 after infection. During each period, a representative sample was taken from the food offered and analysed for dry matter (DM), ash, and CP content (Ministry of Agriculture, Fisheries and Food, Department of Agriculture and Fisheries for Scotland and Department of Agriculture for Northern Ireland (MAFF), 1981). For each animal a composite sample of bulked refusals was taken and analysed for DM, ash and CP. Total faecal output for each individual animal was weighed and two composite samples

taken. One sample was analysed for DM and ash and the other was slurried using approximately 5 ml toluene and 20 ml water for CP analysis. The intake of ME, fermentable ME, effective rumen degradable dietary protein and digestible undegraded protein were estimated using calculations from Agricultural and Food Research Council (AFRC, 1993).

The rate of passage of the roughage through the digestive tract was measured using chromium as a marker. The chromium (Cr) was mordanted to the roughage fibre using the method described by Uden *et al.* (1980, 1982). After feeding 30 to 50 g of the Cr-mordanted hay to the animals faecal samples were taken at 8, 11, 17, 23, 30, 38, 48, 72, 96 and 120 h. The concentration of Cr in the faeces was determined using atomic absorption spectroscopy after wet digestion according to the method by Christian and Coup (1954).

Thrice weekly, 10 ml of blood was collected from the jugular vein for measurement of packed cell volume (PCV) and intensity of parasitaemia (Murray *et al.*, 1977; Paris *et al.*, 1982). Once a week mean corpuscular volume (MCV) and mean corpuscular haemoglobin concentration (MCHC) were determined by an automated blood cell counter (ABX Minos, Roche Diagnostica).

Plasma cholesterol and urea were determined using commercial kits and plasma albumin concentration by the standard biuret method using an auto analyser (Technicon, UK).

On the day the experiment finished all animals were slaughtered and skinned. The right carcass half was macerated and a sample of 500 g taken and stored at −20°C. Later, about 200 g of the sample was freeze dried to a constant weight in a high vacuum freeze drier. The dried samples were finely chopped in a liquidizer and subsamples analysed for protein and ether extract (EE; MAFF, 1981). The DM, CP and crude fat gain of the animals during the experimental period were determined by subtracting the values of the baseline control animals.

Statistical analysis

All measurements, except intensity of parasitaemia and intakes of the diet components, were subjected to statistical analysis using a randomized-block design with each block consisting of a pair of lambs (one I, one PC). Mean effect over time was calculated and subjected to split-plot analysis of variance with consideration of variation between treatments, between animals within treatments and interaction between treatments. Differences in intakes of the diet components in the infected lambs pre- and post-infection were also tested using the block design mentioned above with each block consisting of a pair of pre- and post-infection measurements. Intensities of parasitaemia were evaluated by the non-parametric Mann-Whitney test. Growth rates were determined using linear regression analysis.

The model of Dhanoa *et al.* (1985) was used to analyse the Cr excretion data, which contains an exponential term and a double exponential term derived by considering digesta flow as a multi-component exponential process:

$$y = Ae^{-k_1 t}e^{-Be^{-(k_2-k_1)t}}$$

where y is Cr concentration, A and B are constants, k_1 and k_2 are rate constants and t is the time of

Table 2 *Organic matter (OM), metabolizable energy (ME), fermentable metabolizable energy (FME), crude protein (CP), effective rumen degradable dietary protein (ERDP), digestible undegraded protein (DUP) and metabolizable protein (MP) intake of* T. congolense *infected sheep (no. = 4) given either diet B (r = 0·05, M/D = 9·5, y = 9·5, L = 1·4 to 1·7)† or L (r = 0·08, M/D = 10·1, y = 10·5, L = 2·2 to 2·7) during the pre- (day −14 to 0) and post- (day 1 to 56) infection periods*

Diet	OM (g/kg $M^{0.75}$/day)	ME† (MJ/day)	FME† (MJ/day)	CP (g/day)	ERDP† (g/day)	DUP† (g/day)	MP† (g/day)
Pre-B	66·7	8·1	7·6				
Post-B	62·5	7·9	7·4				
Pooled s.e.	1·63	0·15	0·14				
Pre-L	94·9	13·2	12·0				
Post-L	79·4	12·9	11·8				
Pooled s.e.	3·86	0·63	0·55				
Significance							
Diet effect							
Period effect							
Interaction							

† Calculated using the AFRC (1993) methods where r = rumen digesta fractional outflow rate per h; M/D = MJ metabolizable energy per kg dry matter; L = level of feeding as a multiple of MJ ME for maintenance; y = microbial protein yield in the rumen (g MCP per MJ FME).

Table 3 *Organic matter (OM) and crude protein (CP) apparent digestibility of* T. congolense *infected (I) sheep (no. = 4) and their respective pair-fed controls (PC) given either diet B or L during period 1 (day −10 to −3), period 2 (day 19 to 26) and period 3 (day 50 to 57)*

	OM apparent digestibility			CP apparent digestibility		
Period	1	2	3		2	3
BI	0·62	0·60	0·61	0·66	0·64	0·59
BPC	0·60	0·64	0·67	0·68	0·68	0·67
Pooled s.e.	0·008	0·010	0·014	0·008	0·012	0·019
LI	0·73	0·72	0·72	0·74	0·70	0·71
LPC	0·72	0·76	0·76	0·72	0·74	0·75
Pooled s.e.	0·006	0·009	0·010	0·007	0·010	0·015
Significance†						
Diet effect	**	**	**		**	**
Infection effect		**	**		**	**

† There was no significant interaction effect ($P > 0.05$).

sampling. The rate constants k_1 and k_2 are outflow rate constants for the two largest compartments in the digestive tract likely to be the rumen and possibly the caecum. Mean retention time (MRT) is the mean time between the time of Cr administration and the appearance of Cr in the faeces. The transit time (TT) or lag time is the time between Cr administration and the first appearance of Cr in the faeces (Dhanoa *et al.*, 1985).

Results

Food intake

Although the OM intake of the sheep on diet L was much higher than that of the sheep on diet B ($P < 0.01$; Table 2) the sheep in both dietary groups consumed similar amounts of dietary fibre. The pre-infection values of neutral-detergent fibre (NDF) intakes for diet B and L were 461 (s.d. 28·5) and 417 (s.d. 38·1) g/day respectively and the values for acid-detergent fibre (ADF) intakes were 255 (s.d. 17·9) and 266 (s.d. 29·4) g/day respectively. The ME supplied by diet L was approximately 5 MJ/day higher than that supplied by diet B. The MP supplied by diet L was approximately twice the amount supplied by diet B (Table 2).

The OM intake of the infected animals dropped after infection but the fall was greater in the infected animals given diet L ($P < 0.01$). The depression in OM intake in the lambs given diet L was most pronounced between day 12 and 21 after infection. All lambs finished their daily ration of concentrates before and after infection.

Due to the decrease in OM intake after infection the individual energy and protein components of the diet also decreased. Except for fermentable ME ($P < 0.05$) these decreases were not statistically significant (Table 2).

Calculating the microbial CP supply from both the fermentable ME and effective rumen degradable dietary protein supplies (AFRC, 1993) revealed that in diet B the effective rumen degradable dietary protein was limiting the microbial CP supply whereas in diet L the fermentable ME was limiting the microbial CP supply. These results were hardly affected by the *T. congolense* infection.

It was observed that the lambs on the barley straw (diet B) consumed most of their daily intake just after the morning and afternoon feeding. In contrast, the intake of the lambs on the lucerne hay (diet L) was more spread over the 24-h period.

Apparent digestibility of the diets

The OM apparent digestibility was approximately 10 units higher in diet L than in diet B ($P < 0.01$; Table 3). The OM apparent digestibility remained stable in the I groups on both diets throughout the experimental period. However, OM apparent digestibilities increased by 4 to 6 units in the PC animals as the experiment progressed ($P < 0.01$). The concentrate to roughage ratios did not change much in the animals given diet B but increased in the lambs given diet L from 0·43 in digestibility period 1 to 0·63 in digestibility period 2. In digestibility period 3 the ratio returned to 0·51.

The CP apparent digestibility was approximately 8 units higher in the lambs given diet L compared with those on diet B ($P < 0.01$; Table 3). Whereas the CP apparent digestibilities remained stable in the PC lambs throughout the trial period the apparent digestibilities of the CP in the I lambs decreased

Table 4 *Mean retention time (MRT; h), transit time (TT; h) and rate constants* (k_1, k_2; per *h) of chromium-mordanted roughage offered on day 37 post infection to* T. congolense *infected (I) sheep (no. = 4) fed either diet B or L and their respective pair-fed controls (PC)*

Group	MRT	TT	k_1	k_2
BI	62·67	14·50	0·024	0·177
BPC	55·36	12·97	0·028	0·213
Pooled s.e.	3·33	0·49	0·002	0·017
LI	43·86	13·14	0·040	0·210
LPC	40·67	10·19	0·040	0·211
Pooled s.e.	1·33	0·85	0·001	0·027
Significance†				
Diet effect	*	**		
Infection effect	**	*		

† There was no significant interaction effect ($P > 0.05$).

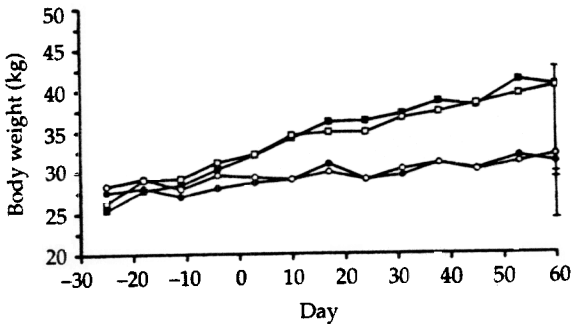

Figure 1 Body-weight changes (kg) of *T. congolense* infected (I) sheep given diet B –●– or L –■– and their respective pair-fed controls (PC) –○– and –□– (no. = 4).

($P < 0.01$). The effects of diet and infection on the OM and CP apparent digestibilities were additive.

Rate of passage of the roughage

The MRT of the animals given diet B was significantly longer than those of the animals given diet L ($P < 0.05$) which appeared to be caused by a lower outflow rate constant k_1 ($P < 0.01$) in the animals given diet B (Table 4).

Both the MRT ($P < 0.01$) and TT ($P < 0.05$) were significantly longer in the I animals compared with the PC. The rate constants k_1 and k_2 did not appear to have been affected significantly by the infection. No significant interaction effects of diet and infection on any of the rate of passage measurements were found (Table 4).

Body weight

The body-weight changes of the PC followed the changes of their I counterparts closely (Figure 1). Growth rates were 50·9 (s.d. 3·0), 37·7 (s.d. 3·8), 184·9 (s.d. 14·7) and 159·4 (s.d. 20·0) g/day for the BI, BPC, LI and LPC groups, respectively. Growth was significantly affected by nutrition ($P < 0.01$) but not by the *T. congolense* infection.

Carcass composition

The carcass of the group given the B diet had a significantly lower DM content than the diet L group ($P < 0.01$; Table 5). The type of diet affected both the fat and protein content ($P < 0.01$) of the carcass, with the animals given diet L showing the higher ether extract, but the lower protein content per kg DM. Total carcass DM, EE and CP gain were significantly higher in the lambs given diet L ($P < 0.01$).

Infection resulted in significantly lower DM content and total carcass DM gain ($P < 0.05$). The total carcass DM gain was about 500 g lower in the I compared with the PC. EE and CP contents of the carcass were not significantly different between the I and PC. Total carcass EE and CP gains were lower in the I groups compared with their PC counterparts, however, differences were not statistically significant (Table 5).

No interaction was found between the diet and infection on any of the carcass measurements.

Parasitaemia

Although the first parasitaemic wave occurred at a similar time in both groups, the number of trypanosomes found appeared to be lower in the LI than in the BI (Figure 2). The second peak of parasitaemia in the LI group started earlier and was higher than the parasitaemia in the BI group which gradually increased to its second peak. After that, the intensities of parasitaemia fluctuated in both groups. None of the differences between the dietary groups was found to be statistically significant.

Table 5 *Carcass dry matter (DM (g/kg fresh matter (FM)), ether extract (EE (g/kg DM)) and crude protein (CP (g/kg DM)) composition and total carcass DM (g), EE (g) and CP (g) gain† of* T. congolense *infected (I) sheep (no. = 4) and their respective pair-fed controls (PC) given either diet B or L*

Group	DM (g/kg FM)	EE (g/kg DM)	CP (g/kg DM)	(Total carcass gain (g)) DM	EE	CP
BI	342·1	375·1	457·3	1415·0	738·3	456·3
BPC	375·8	405·0	438·6	1965·5	1091·4	615·7
Pooled s.e.	8·8	16·4	13·8	234·4	160·0	71·9
LI	432·7	536·1	326·2	5251·9	3483·7	1146·9
LPC	451·5	542·8	327·0	5726·9	3796·3	1307·8
Pooled s.e.	7·0	7·8	6·6	320·6	219·2	92·3
Significance‡						
Diet effect	**	**	**	**	**	
Infection effect	*			*		

† Gain compared with the baseline control animals.

‡ There was no significant interaction effect ($P > 0.05$)

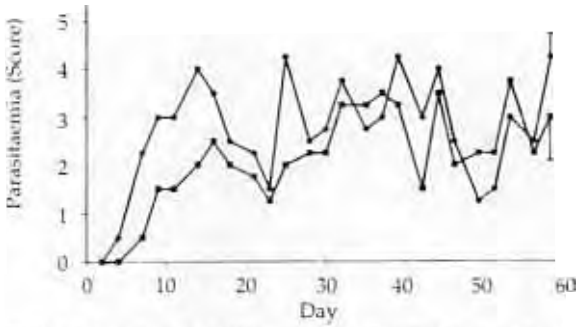

Figure 2 Intensity of parasitaemia of *T. congolense* infected (I) sheep given diet B –●– or L –■– (no. = 4).

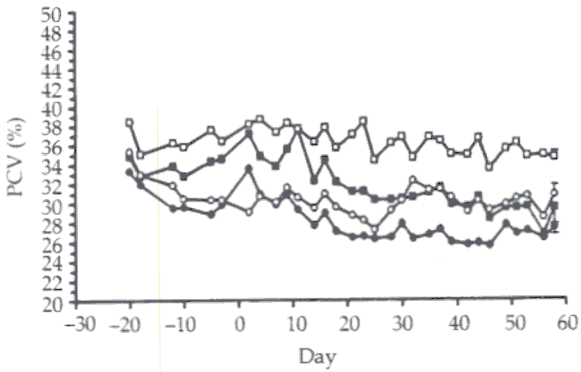

Figure 3 Packed cell volume (%) of *T. congolense* infected (I) sheep given diet B –●– or L –■– and their respective pair-fed controls (PC) –○– and –□– (no. = 4).

Packed cell volume

The PCV before infection was found to be significantly lower in the lambs given diet B ($P < 0.01$) and tended to be lower in the group I lambs compared with the PC group ($P < 0.05$; Table 6). After infection the PCV of the lambs on both diets showed a gradual decrease from approximately day 10 to day 20 after which the PCV stabilized at around 30% for the LI group and 27% for the BI group (Figure 3). The PCV was affected by both infection ($P < 0.01$) and diet ($P < 0.01$). PCV in the LI lambs seemed to be more affected by the infection than the BI (Figure 3) but no interactive effect between infection and diet was found.

Mean corpuscular volume

The MCV did not appear to be significantly affected by nutrition (Table 6). *T. congolense* infection resulted in a slight rise of MCV in the I groups on both diets ($P < 0.05$). The MCV in the PC groups also showed a slight increase during the trial period.

Table 6 *Packed cell volume (PCV, %), mean corpuscular volume (MCV, fl) and mean corpuscular haemoglobin concentration (MCHC, g/dl) of* T. congolense *infected (I) sheep (no. = 4) and their respective pair-fed controls (PC) given either diet B or L during pre- (day −20 to −3) and post-infection (day 14 to 56)*

	PCV		MCV		MCHC	
Group	Pre-	Post-	Pre-	Post-	Pre-	Post-
BI	30·5	26·9	26·3	28·9	36·4	35·6
BPC	31·9	29·9	27·3	28·3	36·7	36·5
Pooled s.e.	0·8	0·8	0·3	0·2	0·2	0·2
LI	33·9	30·5	26·8	29·4	36·6	36·1
LPC	36·6	35·9	26·8	27·9	36·9	37·1
Pooled s.e.	0·7	1·1	0·3	0·4	0·2	0·3
Significance†						
Diet effect	**	**				
Infection effect	*	**				**

† There was no significant interaction effect ($P > 0.05$).

Table 7 *Plasma cholesterol (mmol/l), urea (mmol/l) and albumin (g/l) concentration of* T. congolense *infected (I) sheep (no. = 4) and their respective pair-fed controls (PC) fed either diet B or L during pre- (day −20 to −3) and post-infection (day 14 to 58)*

	Cholesterol		Urea		Albumin	
Group	Pre-	Post-	Pre-	Post-	Pre-	Post-
BI	1·06	0·91	7·3	9·4	28·3	27·3
BPC	1·08	1·27	7·4	7·2	28·3	28·9
Pooled s.e.	0·07	0·10	0·3	0·5	0·3	0·3
LI	0·76	0·79	9·8	10·3	30·3	29·4
LPC	0·76	0·94	10·7	9·2	30·7	30·7
Pooled s.e.	0·04	0·06	0·4	0·4	0·3	0·4
Significance†						
Diet effect	*		**		**	**
Infection effect		**				*

† There was no significant interaction effect ($P > 0.05$).

Mean corpuscular haemoglobin concentration

No significant differences in MCHC were found due to nutrition before or after infection. Infection resulted in a significant decrease in MCHC in group I animals on both diets compared with their PC counterparts ($P < 0.01$; Table 6).

Plasma cholesterol concentration

Plasma cholesterol concentration was lower in lambs on the lucerne hay than those on the barley straw diet ($P < 0.05$; Table 7). The plasma cholesterol levels in the PC and I group on diet B were still rising during the pre-infection period. Infection significantly lowered plasma cholesterol concentrations ($P < 0.01$; Table 7). Figure 4 shows that there was a sharp decrease in plasma cholesterol

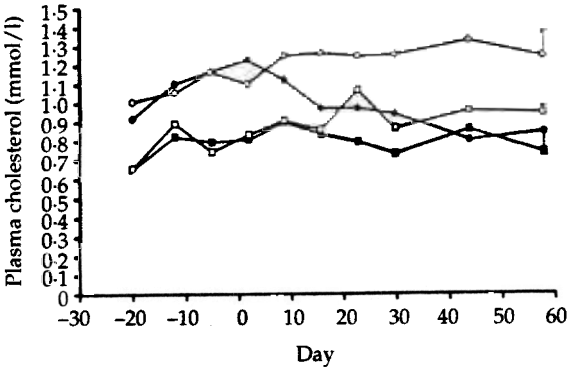

Figure 4 Plasma cholesterol concentration (mmol/l) of *T. congolense* infected (I) sheep given diet B –●– or L –■– and their respective pair-fed controls (PC) –○– and –□– (no. = 4).

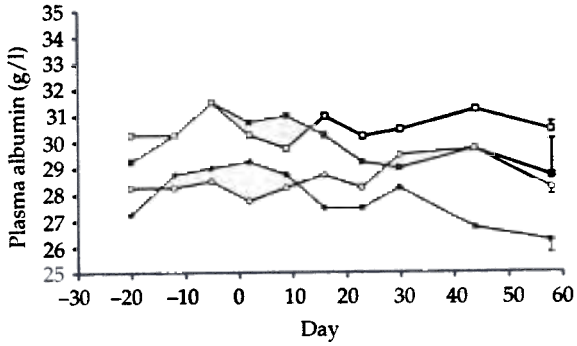

Figure 6 Plasma albumin concentration (g/l) of *T. congolense* infected (I) sheep given diet B –●– or L –■– and their respective pair-fed controls (PC) –○– and –□– (no. = 4).

immediately after infection in the BI group which appeared to stabilize at the same level as the control animals given diet L. However, no significant interaction was found between diet and infection on plasma cholesterol concentration (Table 7).

A relationship was found between the average plasma cholesterol concentration before infection and the average intensity of parasitaemia during the 1st month after infection (r = 0·90; $P < 0·01$). However, one has to take into account that the intensity of parasitaemia was not normally distributed.

Plasma urea concentration

A strong nutritional effect was found before infection on plasma urea concentration ($P < 0·01$; Table 7). A sharp decrease in plasma urea concentration in both the LI and LPC groups was detected around day 23 possibly due to the food intake depression at that time (Figure 5). Plasma urea concentration increased around day 7 after infection, especially in the LI lambs. Infection significantly increased plasma urea concentrations ($P < 0·01$). The nutritional and interaction effects on plasma urea concentration were not significant after infection.

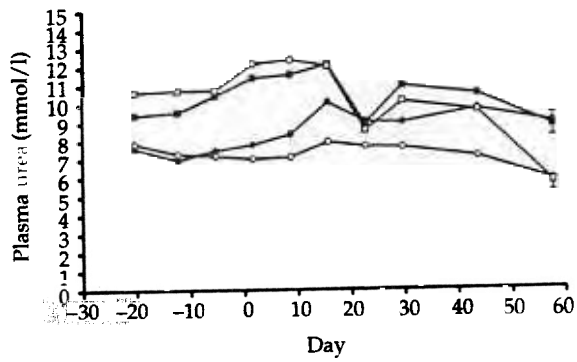

Figure 5 Plasma urea concentration (mmol/l) of *T. congolense* infected (I) sheep given diet B –●– or L –■– and their respective pair-fed controls (PC) –○– and –□– (no. = 4).

Plasma albumin concentration

A significant difference in plasma albumin concentration was detected between lambs on diet B and L ($P < 0·01$; Table 7). Infection resulted in a decrease in plasma albumin concentration in the I groups given both diets ($P < 0·05$) but the nutritional effect was still greater ($P < 0·01$; Figure 6). The effects of nutrition and infection on plasma albumin concentration were additive (Table 7).

Discussion

In this experiment the influence of the type of roughage on digestive function was studied in sheep infected with *T. congolense*. The results showed that digestive function was altered in both dietary groups by the *T. congolense* infection. The MRT was longer and the OM and CP apparent digestibilities were lower in the infected lambs than in their pair-fed counterparts. However, no differences could be observed between body-weight changes of infected lambs and their pair-fed controls. Differences in the diet resulted in differences in PCV, and plasma cholesterol, urea and albumin concentrations. However, the effects of the infection on these measurements were not different between the two dietary groups.

The OM intake of the infected group given diet L was more depressed than the OM intake of the infected group given diet B. The depression in OM intake between day 12 and 21 in lambs on diet L was

probably due to the combination of a slight fall in the quality of lucerne hay and the stress of putting a harness on the animals for the collection of faeces. In contrast, the additional stress did not appear to affect OM intake in the BI animals. These results might have been caused by the difference in type of roughage. Although there was a large difference in DM intake of the lambs between the two diets the total intakes of NDF and ADF were very similar. The first limiting factor on the roughage intake in the lambs on the barley straw is likely to be rumen size, whereas the intake limiting factors in the animals on lucerne hay are more likely to be the metabolites of digestion e.g. propionate (Aitchison *et al.*, 1986; Forbes, 1986; Farningham and Whyte, 1993).

Depressions of voluntary intake were reported by Reynolds and Ekwuruke (1988) in *T. vivax* infected West African dwarf (WAD) sheep given *Panicum maximum* and cassava peel with or without a 1 : 1 mixture of *Leucaena leucocephala* and *Gliricidia sepium*. Depression of voluntary intake of alfalfa pellets was also found during *T. vivax* (Akinbamijo *et al.*, 1992; Zwart *et al.*, 1991; Wassink *et al.*, 1993) and *T. congolense* (Wassink *et al.*, 1993) infections in WAD goats given alfalfa pellets.

The *T. congolense* infected lambs given barley straw showed less intake depression than *T. congolense* infected N'dama heifers given *Andropogon guyanus* hay. The N'dama heifers were also given groundnut cake and groundnut hay which might have affected the *Andropogon guyanus* hay intake (Romney *et al.*, 1994).

The OM digestibility results indicated no direct effect of the infection on OM apparent digestibility but an increase in OM apparent digestibility in the PC lambs ($P < 0{\cdot}01$). In the diet L pair-fed controls this increase in OM apparent digestibility can be attributed to the increased proportion of concentrate to forage. The increase in OM apparent digestibility in the diet B pair-fed controls cannot be explained by changes in the concentrate to forage ratio but may be a consequence of these lambs not being able to eat *ad libitum*. The lack of an increase in OM apparent digestibility in the infected lambs indicates an effect of parasitism. Verstegen *et al.* (1991) did not find any differences in DM apparent digestibility between *T. vivax* infected WAD goats and their controls, but their controls were not pair-fed.

The *T. congolense* infection resulted in a decrease in CP apparent digestibility ($P < 0{\cdot}01$). The data represent the total input/output CP situation and does not partition the effective rumen degradable dietary protein (ERDP) and digestible undegraded protein (DUP) fractions. The fact that in diet B ERDP was limiting the microbial CP supply whereas in diet L the fermentable ME was limiting the microbial CP supply did not appear to have influenced the outcome of the infection on CP apparent digestibility. Reduced apparent digestibility of nitrogen has been observed in lambs infected with the intestinal parasites *Trichostrongylus colubriformis* (Poppi *et al.*, 1986; Kimambo *et al.*, 1988) and a concurrent infection with *T. colubriformis* and *Ostertagia circumcincta* (Bown *et al.*, 1991). These authors implicated increased plasma protein, epithelial cell desquamation and mucus secretion as the source of increased endogenous nitrogen. In certain *T. vivax* isolates which produce an acute syndrome resulting in death within 2 to 3 weeks of infection, massive haemorrhages into the alimentary tract have been found (Hudson, 1944; Mwongela *et al.*, 1981). These haemorrhages are likely to cause loss of endogenous nitrogen. However, in contrast to *T. vivax*, *T. congolense* does not have the capacity to invade tissues of domestic ruminants (Murray and Dexter, 1988). The increase in plasma urea concentration in the infected animals during the present experiment may have been linked to the increase in faecal nitrogen excretion. However, one might expect more urea to be recycled when the MRT is longer. The increase in plasma urea concentration was more pronounced in the *T. congolense* infected lambs given barley straw which was possibly due to the fact that the food energy level was too low to enable all the urea nitrogen to be utilized by the rumen micro-organisms.

As expected, the animals on diet B had a longer MRT than the animals given diet L which was due to a significantly lower outflow rate constant k_1 ($P < 0{\cdot}01$) and which is considered to be the rumen outflow rate constant (Aitchison *et al.*, 1986). The MRT of the roughage was significantly longer in the infected animals than in their respective pair-fed counterparts ($P < 0{\cdot}01$). The results indicate that the longer MRT in the infected lambs was due to a slower rate of passage throughout the entire digestive tract. In previous experiments, van Miert *et al.* (1986) found inhibition of ruminal contractions during the acute phase response in *T. vivax* infected goats, whereas Veenendaal *et al.* (1976) did not find a significant inhibition of the forestomach contractions in *T. vivax* infected goats.

The body-weight gains of the lambs were similar to those predicted by the requirements of housed, castrated lambs published by the AFRC (1993), around 50 g/day for the lambs on diet B and around 200 g/day for those on diet L. The body-weight changes of the infected animals in both dietary groups were not significantly different from their pair-fed control counterparts.

In the present experiment carcass DM content and total carcass DM were significantly lower in the infected animals compared with their pair-fed controls on both diets ($P < 0.05$). One possible explanation may be that the lower plasma albumin concentration in the infected animals caused oedema (Bland, 1956) which in turn might have lowered the carcass DM content. The lower carcass DM led to lower total carcass CP and EE in the infected lambs compared with the pair-fed controls, although this was not statistically significant ($P > 0.05$) due to the variation in differences between the pairs. Katunguka-Rwakishaya (1992) found lower total carcass protein and fat in *T. congolense* infected sheep given two levels of protein but this appeared to be mainly due to differences in carcass weight.

The dramatic increase in maintenance requirements reported by Verstegen *et al.* (1991) in *T. vivax* infected WAD goats was not obvious in this experiment. However, the lower carcass DM gain and hence the lower energy retention may suggest higher maintenance requirements in infected animals.

The first two peak parasitaemias tended to be higher in the BI than in the LI. Otesile *et al.* (1991) found that pigs on a low energy diet developed significantly higher intensities of parasitaemia than those on the high energy diet. Similar tendencies, though not significant, were found by Katunguka-Rwakishaya (1992) in *T. congolense* infected sheep. No difference in intensity of parasitaemia could be attributed to the plane of nutrition, maintenance and submaintenance, in *T. vivax* infected WAD sheep (Reynolds and Ekwuruke, 1988). The theory that the parasites are affected by the nutritional status of the host is not supported by the results of these experiments. However, a significant relationship was found between the plasma cholesterol concentration before infection and the average intensity of parasitaemia during the 1st month after infection ($r = 0.90$; $P < 0.01$). A tendency for higher intensities of parasitaemia with higher plasma cholesterol concentrations was also found in Katunguka-Rwakishaya's (1992) experiment in Scottish Blackface sheep. It is likely that a higher host plasma cholesterol concentration is beneficial to parasite growth and multiplication. Traore-Leroux *et al.* (1987) found significantly higher high-density lipoprotein cholesterol levels in trypanosensitive (zebu cattle than in trypanotolerant Baoule cattle. Since cholesterol levels in the blood are partly heritable (Arave *et al.*, 1974) cholesterol levels might play an important rôle in trypanotolerance.

Diet significantly affected PCV ($P < 0.01$). Agyemang *et al.* (1990, 1992) found lower PCV levels in N'dama cattle kept under field conditions as the dry season progressed due to poorer nutrition. Abdullahi *et al.* (1986) also observed low PCV concentrations in protein deprived sheep.

The PCV was affected by both the *T. congolense* infection ($P < 0.01$) and nutrition ($P < 0.01$). The anaemia was only moderate. Although the effect of the trypanosome infection appeared to be higher in the L-fed animals no interaction was found between nutrition and infection on PCV. Katunguka-Rwakishaya (1992) found that the PCV in the *T. congolense* infected Scottish Blackface lambs given a low-energy diet was more affected than in the animals on a high-energy diet. In ovine fascioliasis, animals on a lower level of protein showed a greater decrease in PCV than animals on a higher level of protein (Berry and Dargie, 1976). In contrast, no differences were observed of PCV in *T. congolense* infected sheep on two levels in protein (Katunguka-Rwakishaya *et al.*, 1993). However, in none of these experiments were measurements made of dietary effects on PCV before infection.

The increase in MCV ($P < 0.05$) and decrease in MCHC ($P < 0.01$) in the *T. congolense* infected animals shows that the anaemia was both macrocytic and hypochromic. The macrocytic and hypochromic responses were similar in both dietary groups. The low digestible CP intake in the BI animals did not result in a lower erythropoietic response compared with the LI animals. Reissman (1964) found that erythropoiesis was markedly reduced in the presence of low protein intake. Katunguka-Rwakishaya *et al.* (1993) reported a dietary effect in that the increase in MCV was much higher in *T. congolense* infected Scottish Blackface sheep given a diet high in protein than in those given a low protein diet. Berry and Dargie (1976) also found a positive response to protein supplementation in both the MCV and MCHC in ovine fascioliasis. Taking the moderate anaemia into consideration, it is possible that in the present experiment the protein offered in the concentrate to the lambs given diet L was enough to support an increase in erythropoiesis. The CP intake of the lambs on the low-protein diet in the experiment of Katunguka-Rwakishaya *et al.* (1993) was only 81 g/day whereas in this experiment it was about 100 g/day.

The cholesterol concentration was higher in the animals on diet B ($P < 0.05$). Katunguka-Rwakishaya (1992) reported significantly higher plasma cholesterol concentrations in Scottish Blackface sheep on a low-energy diet compared with those on a high-energy diet. As reported by Katunguka-Rwakishaya (1992), plasma cholesterol levels decreased markedly ($P < 0.01$), immediately after infection, especially in

the LI group suggesting direct uptake of cholesterol by trypanosomes.

Plasma urea concentrations followed digestible CP intake closely ($P < 0.01$). Infection resulted in an increase in plasma urea concentration especially in the BI group possibly indicating catabolism of body protein in the BI group post infection. These results are comparable with the findings of Abbott *et al.* (1986) in ovine haemonchosis at two levels of protein intake.

Plasma albumin concentrations were also significantly affected by nutrition ($P < 0.01$). Katunguka-Rwakishaya *et al.* (1993) found higher albumin concentration in Scottish Blackface sheep given higher levels of protein. The plasma albumin concentration was more affected by nutrition than by trypanosomiasis and the effects were additive. Plasma albumin concentrations were found to be significantly lower in the *T. congolense* infected Scottish Blackface sheep given a diet low in protein (Katunguka-Rwakishaya *et al.*, 1993). A greater fall in serum albumin concentration was also recorded during ovine haemonchosis (Abbott *et al.*, 1986) and ovine fascioliasis (Berry and Dargie, 1976) in sheep given a diet low in protein compared with those on a high-protein diet.

In conclusion, there is strong evidence that digestive function was altered by the *T. congolense* infection. While the MRT was longer in the infected animals their OM and CP apparent digestibilities were lower than in their pair-fed counterparts. Despite these results no difference could be observed between body-weight changes of infected lambs and their pair-fed controls, although carcasses of the infected lambs had lower DM contents. The effects of the *T. congolense* infection on PCV, cholesterol, urea and albumin, which were relatively mild in this experiment, were affected by the type of roughage and possibly these were due to differences in energy intake. These effects were additive rather than interactive to the effects of infection.

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