

The effects of work and two planes of nutrition on trypanotolerant draught cattle infected with *Trypanosoma congolense*

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Abstract

Thirty-two N'Dama bulls aged 3 to 4 years were used to study the interactions between work, trypanosomosis and nutrition. The bulls were randomly allocated to two treatments, working (W) and non-working (N). Half in each treatment were placed on an andropogon hay basal diet (B), the other half on a better quality groundnut hay diet (H). Five days a week, four pairs of animals in the BW group and four pairs in the HW group pulled weighted sledges four times around a 2056-m track. Loads were set to ensure energy expenditure was equivalent to 1.4 times maintenance. After 4 weeks all 32 bulls were injected intradermally with 10^4 *Trypanosoma congolense* organisms. The trial continued for a further 8 weeks.

Trypanosome infection caused a significant ($P < 0.001$) decline in packed cell volume (PCV), and the anaemia was more severe ($P < 0.05$) in working animals; three pairs in the HW group and two pairs in the BW group were withdrawn because PCV fell below 17%. Diet had no effect on PCV or parasitaemia. Infection caused a decline in food intake ($P < 0.001$) but with significant interactions between diet and work. Intake patterns were similar in the BN and BW groups whilst the HW animals consumed significantly more groundnut hay compared with the HN group ($P < 0.01$). However, nutrition had no significant effect on lap times or the team's ability to work under trypanosomosis challenge. Post-infection, diet was the dominant factor determining weight change, HN and HW animals weighed significantly more than BN and BW animals ($P < 0.01$) and the interaction between period, diet and work demonstrated that BW had the lowest weights in the latter stages of the trial ($P < 0.05$).

The results suggest that supplementation with better quality forages confers no benefit to an animal infected with trypanosomes. Nor can trypanotolerant cattle sustain long periods of work if subjected to a primary challenge of trypanosomes.

Keywords: cattle, nutrition, trypanosomiasis, work.

Introduction

In sub-Saharan Africa expanding human populations have resulted in increased pressure for croplands and a concurrent requirement for an increase in livestock and crop production. The promotion of draught animals within a mixed livestock cropping system is a means of increasing the area cultivated and crop yields. However, a constraint to the expansion of draught animals within the region is the presence of tsetse transmitted trypanosomosis. The use of the N'Dama breed of cattle which exhibit

an innate resistance to trypanosomosis (Roberts and Gray, 1973; Murray *et al.*, 1981) is an option for tsetse endemic areas.

Nutrition is a major problem for draught animals. While draught cattle have the advantage of being able to utilize poor quality forages and crop residues, the peak periods of work are concentrated within the time of greatest food scarcity i.e. at the end of the dry season and beginning of the rains. Farmers in The Gambia respond to this constraint by storing comparatively large quantities of groundnut hay (*Arachis hypogaea*). The hay is given as a supplement throughout the dry season and early rains to maintain body condition and weight in draught cattle.

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It has been suggested that work could increase the susceptibility of draught animals to disease (Starkey, 1981; Munzinger, 1982). Murray *et al.* (1983) reported that the trypanotolerant mechanism can be reduced by stress factors such as work, pregnancy, lactation, inter-current disease and inadequate nutrition. Certainly there is now considerable evidence that plane of nutrition and the degree of nutritional stress play a significant rôle in the ability of trypanotolerant animals to control anaemia during the course of a trypanosome infection (Agyemang *et al.*, 1990; Romney *et al.*, 1997). However, detailed information on the effects of infection on work is limited. There is certainly anecdotal evidence from farmers that draught cattle succumb to the disease during periods of intense work. Similarly, in the 1940s, the first attempts to demonstrate the value of ox drawn equipment to Gambian farmers failed because the animals were reported to suffer badly from trypanosomosis (Sumberg and Gilbert, 1992).

If guidelines for feeding draught cattle in tsetse endemic areas are to be developed, a better understanding of the interaction between work, trypanosomosis and nutrition is needed. Thus the objective of this trial was to investigate the effect of nutrition and work on cattle artificially infected with *Trypanosoma congolense* using diets that reflected existing feeding strategies in The Gambia, where draught bulls are given diets dominated by groundnut hay and poor quality native pasture.

Material and methods

Experimental design

Treatments and animals. Thirty-two N'Dama bulls, aged 3 to 4 years, were selected for the study from an original group of 41, on the basis of their live weight (LW) and willingness to work. Because LW at the start of the trial ranged from 174 to 214 kg, animals were allocated to two subgroups consisting of the 16 lightest and the 16 heaviest with mean live weights of 181 (s.e. 1.68) and 203 (s.e. 1.48) kg respectively. The animals from the two subgroups were then randomly allocated to two treatments, working (W) and non-working (N). Half the animals in each of the two treatments were placed on a basal diet (B), of predominantly andropogon (*Andropogon gayanus*) hay and the other half, on a better quality diet (H) dominated by groundnut hay. This ensured that there was an equal distribution of heavy and light animals in the four treatments, basal non-working (BN), basal working (BW), high non-working (HN) and high working (HW). There was also an additional pair of animals on the HW diet that was used to pull an ergometer to measure work loads (team 9).

Work treatments. The animals in groups HW, BW were given a controlled amount of work to undertake. They worked in pairs pulling weighted metal sledges round a 2056-m track, four circuits a day, 5 days/week (Monday to Friday), for the 12-week duration of the trial. Drivers were allocated to teams at random at the start of the experiment and remained with the same team for the duration of the trial barring accident or illness. Work started at about 09.00 h and continued until each team had completed four circuits of the track. The teams started at 2-min intervals and were encouraged to work at their own pace, overtaking as appropriate. If any team took more than 1 h to complete a single lap of the track, it was withdrawn from work for the remainder of that day.

The sledge loads were initially set at 17% of the combined LW of each team based on the LW at the start (week 1). This was reduced to 10% in weeks 2 and 3 whilst the bulls became accustomed to work. The work data from these three preliminary weeks were not used in subsequent analysis. From week 4, sledge weights were fixed at 12.5% of the team's LW in week 1 and remained at this level for the rest of the trial. The average draught force required by each team to pull its sledge was measured at the start of week 4 using an ergometer with a load cell (Novatech Ltd) and an odometer (Lawrence and Pearson, 1985). The loads were set to ensure estimated energy expenditure during work was equivalent to 1.4 × maintenance.

Dietary treatments. The quantity of food offered to individual animals was calculated on the basis of the mean LW of the initial sub-groups i.e. 180 and 200 kg. The animals on the basal diets (BN and BW) received the equivalent of 1.2 g dry matter (DM) per kg LW of rice bran (*Oryza sativa*) and 9.6 g DM per kg LW of groundnut hay. Animals on the 'high' diet (HN and HW) received the equivalent of 1.2 g DM per kg LW of rice bran and 17.7 g DM per kg LW of groundnut hay, a level set close to maximum voluntary intake while ensuring there were no groundnut hay refusals in the pre-infection period. All animals were offered chopped andropogon hay *ad libitum* at 1.4 times the previous day's intake. Sesame cake (*Sesamum indicum*) was introduced at a constant 1.9 g DM per kg LW for all treatments from week 8 based on the mean weights of the subgroups at the start of the trial. This was in response to LW losses during infection being greater than expected from the intake data collected, raising the possibility that the lack of protein in the diet was inhibiting rumen function.

The animals were given food and watered individually once all animals had completed their

work, the non-working groups were given food at the same time. The bran (and sesame) was offered first, followed by groundnut hay and finally andropogon. The groundnut hay refusals were collected by 15.00 h, the andropogon refusals were collected the following morning. Table 1 summarizes the diets.

Table 1 Composition of the diets offered

	Foods offered g dry matter per kg live weight			
	Groundnut hay	Andropogon hay	Rice bran	Sesamet
Basal	9.4	<i>ad libitum</i>	1.2	1.9
High	17.7	<i>ad libitum</i>	1.2	1.9

† Introduced from week 8.

Trypanosome infection. At the beginning of week 4 all animals, except team 9, were intradermally injected with 1 ml mice blood containing 10^4 *T. congolense* organisms prepared from a clone derivative of *T. congolense* known as ITC 84 (Dwinger *et al.*, 1992).

Management and health. At the start of the trial all 34 bulls were injected with 1.0% w/v ivermectin (Ivomec: Merck Sharp and Dohme) to eliminate internal and external parasites. All animals were treated with 7.0 mg/kg LW diminazene aceturate (Berenil; Hoechst) 8 weeks post infection. Bulls were retired from work for the remainder of the trial if their blood packed cell volumes (PCV) fell below 17%, a threshold that ensured all animals survived the trial (an animal would also have been withdrawn and treated with Berenil if the PCV had fallen below 15%, although this did not occur).

Measurements and observations

Work. The lap times and number of laps completed were recorded daily for each team, throughout the trial. The distance travelled and work done by team 9 were measured weekly throughout the trial using the ergometer and odometer. The average draught force required by the team to pull the sledge was calculated by dividing the work done by distance travelled. The net energy (NE) expenditure for work of each bull in team 9 was estimated from work done and the distance travelled using the factorial equation developed by Lawrence (1985).

The work done by the other eight teams in the BW and HW treatments was estimated from the distance travelled by the team each day multiplied by the teams' average draught force measured in week 4. Weekly average draught force values were compared with that of team 9 at the start of week 4, when the sledge weights were fixed to ensure they remained

constant throughout the experiment. NE expenditure for each bull was calculated using the factorial equation (Lawrence, 1985). The metabolizable energy (ME) requirements of the bulls were estimated by assuming that the efficiency of utilization of ME for work was the same as for maintenance (k_m) (Matthewman and Dijkman, 1993). ME requirements for work were calculated by dividing NE expenditures by k_m where $k_m = 0.35q_m + 0.503$ and q_m = metabolizability of the diet given (ME/GE) (Agricultural Research Council, 1980). The ME requirement for maintenance (ME_m) of the N'Dama bulls was assumed to be 132.5 kJ/kg LW.

Live weight. Live weights were recorded twice weekly, in the morning before feeding and work.

Food intake refusals and analysis. Voluntary DM intake was recorded daily throughout the trial by weighing food offered and total food refusals. Separate daily subsamples from the food offered and refused were pooled over a 7-day period, dried in an oven at 60°C to constant weight, ground through a 1-mm screen and stored for analysis. The following determinations were made on the weekly pooled samples: DM, organic matter (OM), nitrogen (N), neutral-detergent fibre (NDF) and acid-detergent fibre (ADF). The ME values were taken from the literature.

Haematological measurements. Blood samples were collected thrice weekly from the jugular vein with ethylene diamine tetra-acetic acid coated vacutainers. The samples were examined by the buffy coat dark ground/phase parasitological technique to detect presence of trypanosomes and to quantify the intensity of infection as a parasitaemia score (Murray *et al.*, 1977). The PCVs were determined using the standard microhaematocrit technique.

Statistical analysis

Live weight, food intake and haematological data. The LW and food intake data were divided into three distinct periods, period 1 (pre-infection weeks 1 to 4), period 2 (post-infection weeks 5 to 7) and period 3 (post-infection weeks 8 to 12). The data were analysed using the general linear models (GLM) procedure of the Statistical Analysis Systems Institute (1994). The model included the individual effects of age, weight at the start, period, week (nested within period), diet, work, animal (nested within age, weight at start, diet and work) and period \times animal (nested within age, weight at start, diet and work). The interactions between diet, work and period were tested. A contrast analysis, comparing periods 2 and 3 with period 1, was used to identify the period in which the interaction occurred. Statistical significance was tested using the F test.

Table 2 Effects of diet and work before infection (period 1) and after infection (periods 2 and 3) with *T. congolense* on mean packed cell volume (PCV) (%)

Treatment†			Mean PCV (%) for period			Significance of effects
Diet	Work	Nc	2	3		
B	N	8	30.0	26.6	21.2	Period Week (period) Diet Work Diet × work Period × diet Period × work Period × diet × work Animal
B	W	8	28.9	25.4	18.7	
H	N	8	30.5	27.4	20.8	
H	W	8	29.9	26.4	19.2	
Subclass means						
Diet	B	16	29.5	26.0	19.9	Period × diet × work
	H	16	30.2	26.9	20.0	
Work	N	16	30.2	27.0	21.0	Animal
	W	16	29.4	25.9	18.9	
s.e.			0.56	0.60	0.50	

† Codes are: B = basal; H = supplemented with groundnut hay; W = working; N = non-working.

Using the GLM model described, the least-square means could not be estimated because animals were withdrawn from the trial in periods 2 and 3 resulting in empty cells. The results presented in Tables 2 and 3 are unadjusted means for each treatment with an accompanying standard error of the mean. The data of animals withdrawn from work in period 3 were also included because, with the exception of LW and PCV, there was no significant difference between the means of the 'survivors' and those that were too sick to complete the work programme.

Work output data. Lap times for weeks 4, 5 and 6 to 7 were analysed separately using a balanced multi-way ANOVA to examine the effects of diet, day of the

week, lap and team and their possible interactions. Team mean lap times were further analysed using a two-way ANOVA to look for significant differences between weeks. The post-infection analysis was restricted to weeks 6 and 7 when all teams were being worked; once teams were withdrawn from work there were insufficient replicates in each treatment group for reliable analysis. Week 5 was considered a pre-patent period before the acute phase of infection.

Results

PCV and dark ground scores

All animals became infected with trypanosomes and remained so until treatment with Berenil. Infection

Table 3 Effects of diet and work before infection (period 1) and after infection (periods 2 and 3) with *T. congolense* on mean live weights

Treatment†			Mean live weights (kg) for period			Significance of main effects
Diet	Work	No.	2	3		
B	N	8	188	187	182	Weight at start Period Week (period) Diet Work Diet × work Period × diet Period × work Period × diet × work Animal
B	W	8	188	184	175	
H	N	8	192	193	188	
H	W	8	188	190	184	
Subclass means						
Diet	B	16	188	185	178	Period × diet × work
	H	16	190	192	185	
Work	N	16	190	190	185	Animal
	W	16	188	187	179	
s.e.			2.3	2.4	2.5	

† For treatment codes see Table 2

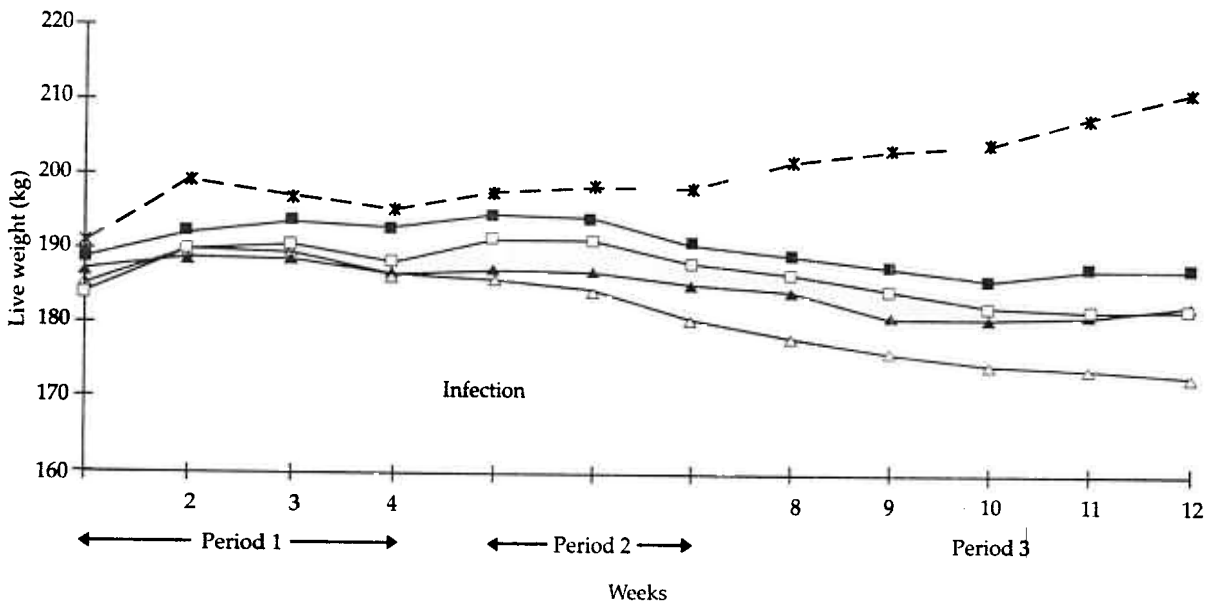


Figure 1 Effects of infection with *T. congolense* and diet on the mean live weights of working (BW (△) and HW (□)) and non-working (BN (▲) and HN (■)) bulls (including team 9 (✱), uninfected).

caused a significant decline in PCV in periods 2 and 3 ($P < 0.001$; Table 2). Diet had no significant effect, whilst in period 3, working animals had significantly lower PCVs ($P < 0.05$). Working animals were less able to control anaemia, five of the eight teams were withdrawn from work because the PCV of one or other of the bulls dropped below 17%; three in the HW group and two in the BW group. No animal was withdrawn from the non-working groups (BN and HN). As expected when the PCV is used as the criterion for withdrawal from work, the mean of the survivors in period 3 was higher than that of those withdrawn, 20.4 (s.e. 0.48) compared with 18.0 (s.e. 0.85), respectively ($P < 0.001$).

The overall mean dark ground (DG) scores in periods 2 and 3 were 3.12 (s.e. 0.08) and 3.46 (s.e. 0.14) and the parasitaemias in period 3 were significantly higher ($P < 0.05$). The lower PCVs in the working animals (BW and HW) were accompanied by significantly ($P < 0.01$) higher DG scores in both periods: 3.37 (s.e. 0.1) compared with 2.88 (s.e. 0.1) in period 2 and 3.86 (s.e. 0.17) compared with 3.05 (s.e. 0.17) in period 3. Diet had no significant effect neither was there any interaction between diet and work on parasitaemia.

Live weight

Pre-infection (period 1), diet and work had no significant effect on LW (Table 3). Post-infection

(periods 2 and 3), all animals lost weight and there were significant interactions between period, diet and work on LW. Animals on the diet dominated by groundnut hay (HN and HW) weighed on average 4.18 (s.e. 1.50) kg more in period 2 and 4.53 (s.e. 1.47) kg more in period 3 ($P < 0.01$) than those on the diet dominated by andropogon hay (BN and BW). Work had no significant effect on LW in the initial stages of infection (period 2) but by period 3 working animals (BW and HW) weighed on average 3.93 (s.e. 1.47) kg less ($P < 0.01$) than their non-working counterparts. By period 3, the interaction of period, diet and work suggested that working animals on the basal diet had significantly the lowest LW at 6.9 (s.e. 2.95) kg less than other groups ($P < 0.05$). Comparison of the LW of the working bulls (BW and HW) indicated that those animals that were withdrawn from the work programme weighed significantly ($P < 0.001$) less in period 1 than those that survived and worked until the end of the trial (182 (s.e. 3.8) kg *v.* 197 (s.e. 3.0) kg).

Figure 1 illustrates the change in mean LW of the four treatment groups and team 9 (uninfected) as the trial progressed. Once sesame had been introduced in week 8, the two bulls in team 9 gained 0.339 (s.e. 0.054) kg/day compared with the infected bulls on similar diets, the HN and HW groups, which lost on average -0.060 (s.e. 0.048) kg/day and -0.165 (s.e. 0.054) kg/day respectively.

Table 4 Nutrient composition of the foods offered and refused

Food	Food composition (g/kg dry matter)					
	Dry matter	Organic matter	Crude protein	Neutral-detergent fibre	Acid-detergent fibre	Metabolizable energy (MJ)†
Groundnut hay (offered)	944	944	81	522	461	10.0
Groundnut hay (refusals)	923	950	55	612	546	
Andropogon (whole plant)	942	962	21	752	503	7.4
Andropogon (leaves)	958	953	27	728	471	
Andropogon (stem)	944	977	8	818	543	
Andropogon (refusals)	926	977	7	838	547	
Rice bran	955	806	52	595	477	11.0
Sesame	962	923	312	221	89	12.4

ME based on literature estimates.

Food intake

Table 4 summarizes the nutrient composition of the foods offered and refused. The results indicate that the bulls rejected components of the diet that contained higher levels of fibre, particularly ADF. Table 5 summarizes the mean food intakes for the three periods and the significance of infection, work, and diet on the different components of the diet. Figure 2 illustrates the pattern of groundnut hay and andropogon intakes in g DM per kg LW.

Groundnut hay. Within the basal groups (BN and BW), daily groundnut hay intake was constrained to

9.6 g DM per kg LW and the animals ate all that was offered throughout the 12-week period irrespective of work or infection (see Figure 2a). However, a different pattern of intake emerged with the HN and HW groups offered 17.7 g DM per kg LW of groundnut hay. In the pre-infection period all groundnut hay was consumed. Infection in period 2 resulted in a significant decline in groundnut hay intake equivalent to -1.23 (s.e. 0.27) g DM per kg LW per day ($P < 0.05$). This decline predominantly occurred within the HN group and persisted into period 3. By period 3 there was also a significant

Table 5 Effects of diet and work before infection (period 1) and after infection (periods 2 and 3) with *T. congolense* on mean daily intake of groundnut hay, andropogon hay, rice bran and sesame

Treatment†		No.	Mean daily intake (g/kg live weight) of different components of the diet in periods 1, 2 and 3											
Diet	Work		Groundnut hay			Andropogon hay			Rice bran			Total dry matter		
			1	2	3	1	2	3	1	2	3	1	2	3
B	N	8	9.6	9.6	9.9	8.0	5.4	3.7	1.0	0.7	1.3	18.6	15.7	16.9
B	W	8	9.6	9.6	10.2	9.6	6.8	5.4	1.1	1.0	1.3	20.3	17.4	19.1
H	N	8	17.5	15.8	14.8	2.4	1.7	1.1	1.2	0.9	1.2	21.1	18.5	19.1
H	W	8	17.9	17.1	17.3	2.6	1.7	0.9	1.2	0.9	1.2	21.7	19.8	21.5
Subclass means														
Diet	B	16	9.6	9.6	10.1	8.8	6.1	4.6	1.1	0.9	1.3	19.5	16.6	18.0
	H	16	17.7	16.5	16.1	2.5	1.7	1.0	1.2	0.9	1.2	21.4	19.1	20.3
Work	N	16	13.6	12.7	12.3	5.2	3.6	2.4	1.1	0.8	1.2	19.9	17.1	18.0
	W	16	13.7	13.4	13.8	6.1	4.2	3.2	1.2	1.0	1.3	21.0	18.6	20.3
	s.e.		0.73	0.63	0.59	0.61	0.44	0.42	0.03	0.07	0.01	0.30	0.33	0.34
Significance of effects														
Period				***			***			***			***	
Week (period)				***			***			***			***	
Diet				***			***						**	
Work				**									*	
Diet × work				*										
Period × diet				***			***							
Period × work				***									**	
Period × diet × work				**										
Animal				***			***			***			***	

† treatment codes see Table 2

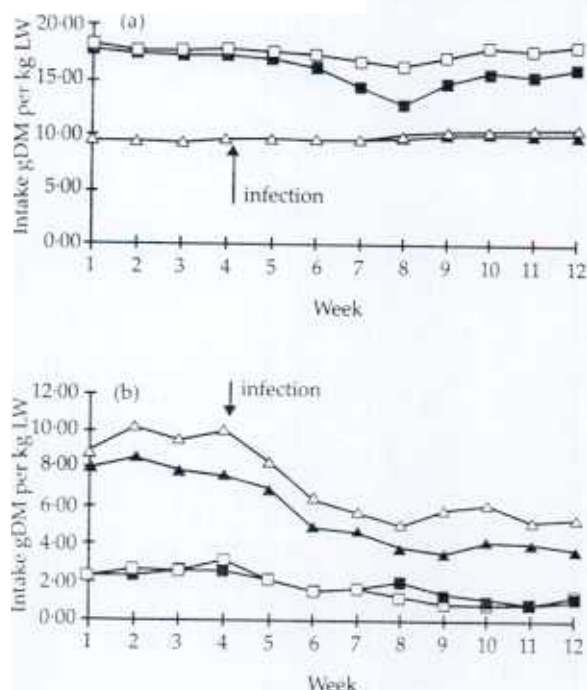


Figure 2 Effects of infection with *T. congolense* on mean weekly (a) groundnut hay and (b) andropogon hay intakes (g dry matter per kg live weight) of working (BW (Δ)) and non-working (BN (\square)) and HN (\blacktriangle)) bulls.

interaction between diet and work with working animals consuming 1.76 (s.e. 0.49) g DM per kg LW more groundnut hay than non-working animals ($P < 0.01$).

Andropogon hay. The andropogon hay, was offered *ad libitum* and the intakes were higher in the basal diets (BN and BW). Whilst work appeared to consistently elevate daily andropogon hay intake in the basal group (BW), the difference was not significant due to a high a degree of variability in intake between individual animals. The pattern of intake and the proportional decline in response to infection was similar when comparing BN and BW groups (see Figure 2b). Overall, infection had a significant ($P < 0.001$) effect on daily andropogon hay intake which declined in periods 2 and 3 by an average of 1.85 (s.e. 0.38) g/kg LW and 2.68 (s.e. 0.36) g/kg LW, respectively. There was no significant interaction between period, diet and work. Eight weeks post infection, there was no evidence of a recovery in andropogon intake.

Rice bran and sesame cake. Rice bran intake declined significantly ($P < 0.001$) in the initial stages of infection (period 2) but recovered in period 3 when sesame was mixed and given with the bran. There were no significant effects of diet or work on bran intake although individual animal intake did vary significantly ($P < 0.001$). All animals ate the sesame cake introduced in period 3.

Table 6 Effects of infection with *T. congolense* on weekly mean lap times for each team expressed as proportions of the time in week 4 when healthy (time in week 4 taken as 1.00)

		Lap times expressed as a proportion of week 4								
Week:		4	5	6	7	8	9	10	11	12
Status:		Healthy	Pre-patent	Infected	Infected	Infected	Infected	Infected	Infected	Infected
Team	Treatment									
1	HW	1.00	0.94	1.03	1.38	1.88	1.69			
2	HW	1.00	0.92	1.16	1.43	1.42				
3	HW	1.00	0.80	1.01	1.24	1.17	1.02	1.09	1.11	
4	HW	1.00	1.09	1.08	1.13	1.46	1.33	1.15	1.19	1.17
5	BW	1.00	1.09	1.35	1.65	1.95				
6	BW	1.00	0.95	1.02	1.52					
7	BW	1.00	0.97	1.00	1.19	1.23	1.16	1.12	1.09	1.07
8	BW	1.00	0.98	1.09	1.22	1.26	1.30	1.19	1.23	1.25
9	Control	1.00	0.97	0.99	1.00	1.04	0.98	0.97	0.94	0.92
Group mean	HW	1.00	0.94	1.07	1.30	1.48	1.35	1.12	1.15	1.17
Group mean	BW	1.00	1.00	1.12	1.40	1.48	1.23	1.15	1.16	1.16

† For treatment codes see Table 2.

Table 7 Mean lap times for all working teams (BW and HW) before and after infection with *T. congolense*

Lap	Mean lap times (min : s)					
	Pre-infection		Pre-patent		Infected	
	Week 4	s.e.	Week 5	s.e.	Weeks 6††	s.e.
1	26:00	00:18	25:34	00:23	31:28	00:47
2	27:13	00:36	26:18	00:40	33:05	00:59
3	27:56	01:02	26:08	00:26	34:36	01:13
4	28:08	00:21	27:21	00:38	34:07	01:05
Significance	*		**		**	
s.e.d.	00:47		00:27		00:57	
No.	40		40		80	

† Lap times of weeks 6 and 7 combined

Total food intake. Post-infection, work had a significant effect on daily total DM intake ($P < 0.05$) whilst diet had a significant effect on total DM intake throughout the trial ($P < 0.01$; Table 5). Animals given the higher levels of groundnut hay (HN and HW) had higher mean daily intakes than those on the andropogon hay basal diet (BN and BW). Infection significantly ($P < 0.001$) reduced total food intake in period 2; the apparent recovery of total intake in period 3 was partly a consequence of the introduction of sesame cake in period 3. In period 3, there was also a significant interaction ($P < 0.01$) between work and period with the working groups (BW and HW) eating 1.15 (s.e. 0.4) g/kg LW of DM more than the non-working groups (BN and HN).

Estimated metabolizable energy and crude protein intakes. Based on the food intake data, the estimated daily ME intake of the BW and HW groups during period 1 was 170 kJ/kg LW and 200 kJ/kg LW respectively. This was equivalent to 1.3 × maintenance for the BW group and 1.5 × maintenance for the HW group. During period 3, the estimated daily ME intake of the BW and HW groups was 173 kJ/kg LW and 207 kJ/kg LW due to the introduction of sesame which allowed the animals to maintain ME intake through an increase in the energy concentration of the diet despite changes in forage intake. The ME concentration (M/D) of the BW diet increased from 8.8 to 9.6 MJ/kg DM, the HW diet correspondingly increased from 9.8 to 10.2 MJ/kg DM.

In period 1, the estimated crude protein (CP) content of the BW and HW diets was 51 g/kg DM and 72 g/kg DM, both marginal to the animals requirements. The introduction of sesame increased the CP content of the BW diet to 96 g/kg DM and in the HW group to 102 g/kg DM.

Work output and energy expenditure

The mean work output of team 9 measured with the ergometer was 2.13 (s.e. 0.030) MJ/day within a range of 2.02 to 2.27 MJ/day. The average draught force required to pull the sledge varied from 244 to 276 N (mean of 258 (s.e. 1.8) N). The mean ME expenditure for work (ME_{work}) of the bulls in team 9 was 10.08 (s.e. 0.946) MJ per head per day or 50 (s.e. 0.4) kJ/kg per day, proportionately 0.38 of the energy requirements of an animal for maintenance. The estimated ME_{work} of the bulls in the other eight teams were very similar ranging from 48 to 58 kJ/kg per day with an overall mean of 53 (s.e. 0.2) kJ/kg per day.

Until the end of week 4 when the bulls were infected, all teams worked well, easily completing their four laps of the track each day. The uninfected pair of bulls (team 9) continued to work well thereafter, completing the 12 weeks of work, and indeed getting fitter as the trial progressed, as indicated by decreasing lap times. In contrast only three of the eight infected teams were able to work for the full 12 weeks of the experiment, because the PCV of one or other of the bulls in the team had dropped to 17%. Three teams on the HW were retired in weeks 9, 8 and 11 respectively, and two teams on the BW treatment in weeks 8 and 7. Table 6 illustrates lap times expressed as a proportion of the lap time immediately prior to infection (week 4).

Comparison of lap times (Table 7) showed that the teams slowed down significantly once the infection was established ($P < 0.001$). The mean lap times during weeks 4 and 5 of 27 min 19 s and 26 min 20 s respectively were not significantly different. However, both were significantly lower than the lap mean during the infected period, 36 min 46 s. Nutrition had no significant effect on lap times or on the ability of a team to work throughout the experimental period.

During the course of a working day there was a significant decline in speed with each successive lap, irrespective of the diet or day of the week (see Table 7). Similarly, once the animals were infected they slowed down over the course of each week from a mean of 29 min 10 s per lap on a Monday to 38 min 2 s by Friday (s.e.d. ± 1 min 30 s) ($P < 0.001$).

Discussion

Gambian farmers start working N'Dama bulls when they weigh between 170 and 200 kg. It can be assumed that the bulls used in this trial are representative of animals in their first working season. The draught force imposed in this trial, an average of 6.5% of LW, was generally less than that

observed on-farm, which ranged from 6.8 to 19.3% of LW (Afford, 1994). The diet initially offered was similar to that used by farmers at the end of the dry season, groundnut hay in varying proportions, poor quality native pasture and limited amounts of bran. Oilseed cakes are generally not available to farmers although the response of team 9 to sesame cake in period 3 illustrates their desirability (Figure 1).

The diet offered to the HN and HW groups was sufficient to satisfy their ME requirements for maintenance and work irrespective of their andropogon hay intake. The BN and BW groups were only able to satisfy their requirements by consuming substantial amounts of andropogon hay. To achieve an ME intake of 1.4 X maintenance, the BW animals would have had to consume about 10 g DM per kg LW of andropogon hay each day, a level of intake approached only in the pre-infection period. The food intake results (Table 5) suggest that prior to infection the BW group had only a slight energy deficit, whilst the HW group had easily sufficient energy for maintenance and the work imposed. The mean CP contents of the diets in periods 1 and 2 were 50 to 70 g/kg DM, marginal to requirements. However, it should be remembered that the diets were initially based on foods available to local farmers. A protein deficit would explain the limited LW gain in the non-working groups (BN and HN) in period 1 and their greater than expected weight loss during infection. Ultimately, sesame cake was introduced into the diet in period 3 in an attempt to stabilize the weight loss, as there was concern that rumen function was impaired.

This trial demonstrated significant changes in food intake in response to infection and the diet offered. Diet quality influenced total food intake; animals in the groups (HN and HW) receiving the higher levels of groundnut hay had significantly ($P < 0.01$) higher food intakes. Infection resulted in a decline in food intakes but there were also significant ($P < 0.01$) interactions between period, diet and work. Both basal groups (BN and BW) had similar patterns of food intake, showing a decline in response to infection, which is consistent with literature reports (Verstegen *et al.*, 1991; Zwart *et al.*, 1991; Romney *et al.*, 1997). A different pattern emerged with the diets containing higher levels of groundnut hay (groups HN and HW). Essentially, animals responding to the demands of work, appeared to be able to maintain food intake during infection if the diet included a higher quality component equivalent to groundnut hay (a legume). While the control mechanism governing food intake during the course of infections is thought to be cytokine mediated (McCarthy *et al.*, 1985; and van Miert *et al.*, 1986), this study demonstrated that the severity of anorexia will vary

depending on the nutrient composition of the diet and the energetic demands of the animal. This suggests that anorexia during trypanosomosis is also affected by physiological and physical intake mechanisms, even if it is induced by cytokines.

The ability of the HW animals to maintain groundnut hay intake at proportionately 0.94 of pre-infection levels would imply that the effects of trypanosomosis on work would be limited compared with the BW animals. Certainly, the levels of intake in the HW group were sufficient for maintenance and work. However, nutrition had no significant effect on lap times or on the team's ability to work throughout the experimental period. Only three of the eight teams infected with trypanosomosis were able to work for the full 12 weeks, two in the BW group and one in the HW group. The teams were retired from work because one or other of the bulls were severely anaemic (PCV < 17%). By period 3 the PCVs of working animals were significantly lower ($P < 0.001$) which was accompanied by higher DG scores.

The lack of a difference in lap times between the working groups suggests anaemia during trypanosomosis infection is possibly the major factor governing work output due to a decline in the oxygen carrying capacity of the blood. Payne *et al.* (1991) questioned whether the maintenance of an elevated body temperature in *T. evansi* infected buffaloes resulted in a reduction in energy available for metabolic activity and work as the metabolic rate of the animal has to be increased. The lack of any difference between the HW and BW groups would imply that this was not a primary factor causing the reduction in work rates in N'Dama bulls.

Pre-infection, diet and work had no significant effect on LW. Post-infection (periods 2 and 3) diet quality was the dominant factor in determining weight change, the animals on the basal diet weighing significantly less by period 2. Work had no significant effect on LW until period 3 when working animals lost significantly more ($P < 0.01$). The significant interaction between diet, work and period (due to the low LW of BW animals in period 3 ($P < 0.05$)) indicates a cumulative effect on LW as the trypanosomosis infection progressed. Previous studies of the interaction between nutrition and trypanosomosis (using the IL1180 strain of *T. congolense*) in N'Dama cattle suggested that weight change was primarily a function of a change in food intake as a consequence of infection and not a change in metabolism (Romney *et al.*, 1997; Akinbamijo *et al.*, 1997). However, there is some indication from this trial that a change in metabolism in response to infection was also responsible for the weight loss.

The mean daily weight loss of -0.060 (s.e. 0.048) g/day exhibited by the HN group in period 3 was evidence of a metabolic cost of infection, considering the estimated ME intake was 36.3 MJ (equivalent to $1.4 \times \text{ME}_m$) and the crude protein content of the diet was 98 g/kg DM. Dwinger *et al.* (1992) and Osaer *et al.* (1994) concluded that ITC 84 is a more virulent strain of *T. congolense* than the IL1180 strain and these results indicate that there is a substantial metabolic cost associated with ITC 84. Authié (1994) reasoned that the virulence of a trypanosome infection could be related to the excessive production of cytokines and the release of secondary compounds into the host's blood stream when successive populations of trypanosomes are lysed by antibodies. If so, virulence is a factor that requires further consideration as it appears to influence the severity of the disease and the host response.

This study has a number of practical implications for farmers and organizations wishing to promote draught N'Dama oxen in areas of high trypanosomosis challenge. The results suggest that supplementation with better quality forages, such as groundnut hay, confers no benefit on the working ability of the animal if infected with trypanosomes. Nor is it likely that trypanotolerant cattle would be able to sustain long periods of work if subjected to a new serodeme of trypanosomes, which agrees with the report by Ravindran *et al.* (1990) in Liberia. Given the importance of draught cattle to the income and food security of smallholder farmers, chemotherapy is necessary for N'Dama cattle if they become infected during the stressful working period. However, further study is required to assess whether the control of trypanosomosis is improved if trypanotolerant draught animals first develop an acquired immunity through the repeated exposure to local strains of the disease. By artificially challenging the bulls with a new strain of trypanosomosis, this trial only tested the innate resistance of the N'Dama, but the trial illustrates the importance of chemotherapy if draught N'Dama cattle are to be promoted in new tsetse endemic areas.

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References

- Agricultural Research Council. 1980. *The nutrient requirements of ruminant livestock*. Commonwealth Agricultural Bureaux, Slough.
- Agyemang, K., Dwinger, R. H., Touray, B. N., Jeannin, P., Fofana, D. and Grieve, A. S. 1990. Effects of nutrition on the degree of anaemia and liveweight changes in N'Dama cattle infected with trypanosomes. *Livestock Production Science* **26**: 39-51.
- Akinbamijo, O. O., Bennison, J. J., Romney, D. L., Wassink, G. J., Jaitner, J., Clifford, D. J. and Dempfle, L. 1997. An evaluation of food intake, digestive physiology and live-weight changes of N'dama and Gobra zebu bulls following experimental *Trypanosoma congolense* infection. *Animal Science* **65**: 151-158.
- Alford, R. J. 1994. Working and feeding strategies of draught N'Dama oxen in a Gambian village. M.Sc. thesis, Centre for Tropical Veterinary Medicine, University of Edinburgh.
- Authié, E. 1994. Trypanosomiasis and trypanotolerance in cattle: a role for congopain? *Parasitology Today* **10**: 360-364.
- Dwinger, R. H., Clifford, D. J., Agyemang, K., Gettinby, G., Grieve, A. S., Kora, S. and Bojang, M. A. 1992. Comparative studies on N'Dama and zebu cattle following repeated infections with *Trypanosoma congolense*. *Research in Veterinary Science* **52**: 292-298.
- Lawrence, P. R. 1985. A review of the nutrient requirements of draught oxen. In *Draught animal power for production* (ed. J. W. Copland), proceedings of an international workshop held in James Cook University, Townsville, Australia, 10-16 July 1985, pp. 59-68. Australian Centre for International Agricultural Research, Canberra.
- Lawrence, P. R. and Pearson, R. A. 1985. Factors affecting measurement of draught force, work output and power of oxen. *Journal of Agricultural Science, Cambridge* **105**: 703-714.
- McCarthy, D. O., Kluger, M. J. and Vander, A. J. 1985. Suppression of food intake during infection: is interleukin-1 involved? *American Journal of Clinical Nutrition* **42**: 1179-1182.
- Matthewman, R. W. and Dijkman, J. T. 1993. The nutrition of ruminant draught animals. *Journal of Agricultural Science, Cambridge* **121**: 297-306.
- Miert, A. S. J. P. A. M. van, Duin, C. T. M. van and Anika, S. M. 1986. Anorexia during febrile conditions in dwarf goats. The effect of diazepam, flurbiprofen and naloxone. *The Veterinary Quarterly* **8**: 266-273.
- Munzinger, P. 1982. *Animal traction in Africa*. GATE GTZ, 120. Friedrich Vieweg & Son, Braunschweig, Wiesbaden.
- Murray, C. M., Murray, M., Murray, P. K., Morrison, W. I., Payne, C. and McIntyre, W. I. M. 1977. Diagnosis of African trypanosomiasis in cattle. Improved parasitological and serological techniques. *Fifteenth meeting of the International Scientific Council for Trypanosomiasis Research and Control*. Publication no. 110 OAU/STRC, The Gambia, pp. 247-254.
- Murray, M., Clifford, D. J., Gettinby, G., Snow, W. F. and McIntyre, W. I. M. 1981. Susceptibility to African trypanosomiasis of N'Dama and zebu cattle in an area of *Glossina morsitans submorsitans* challenge. *The Veterinary Record* **109**: 503-510.
- Murray, M., Trail, J. C. M., Turner, D. A. and Wissocq, W. 1983. *Livestock productivity and trypanotolerance. Network training manual*. International Livestock Centre for Africa (ILCA), Addis Ababa, Ethiopia.

- Osaer, S., Goossens, B., Clifford, D. J., Kora, S. and Kassama, M. 1994. A comparison of the susceptibility of Djallonké sheep and West African dwarf goats to experimental infection with two different strains of *Trypanosoma congolense*. *Veterinary Parasitology* 51: 191-204.
- Payne, R. C., Djahuri, D., Partoutomo, S., Jones, T. W. and Pearson, R. A. 1991. *Trypanosoma evansi* infection in worked and unworked buffaloes (*Bubalus bubalis*) in Indonesia. *Veterinary Parasitology* 40: 197-206.
- Ravindran, S., Massaquoi, R. C. and Wiles, S. 1990. Research for the control of draught animal diseases in West Africa: needs, experiences and methods. In *Research for development of animal traction in West Africa* (ed. P. R. Lawrence, K. Lawrence, J. T. Dijkman and P. H. Starkey), proceedings of the fourth workshop of the West Africa Animal Traction Network, Kano, Nigeria, 9-13 July 1990. International Livestock Centre for Africa, Addis Ababa, Ethiopia.
- Roberts, C. J. and Gray, A. R. 1973. Studies on trypanosome-resistant cattle. II. The effect of trypanosomiasis on N'Dama, Muturu and zebu cattle. *Tropical Animal Health and Production* 5: 220-233.
- Romney, D. L., N'Jie, A., Clifford, D., Holmes, P. H., Richard D. and Gill, M. 1997. The influence of plane of nutrition on the effects of infection with *Trypanosoma congolense* in trypanotolerant cattle. *Journal of Agricultural Science, Cambridge* 129: 83-89.
- Starkey, P. 1981. *Farming with work oxen in Sierra Leone*. Sierra Leone Work Oxen Project, Ministry of Agriculture and Forestry, Njala University College.
- Statistical Analysis Systems Institute. 1994. *SAS/STAT guide for personal computers, version 6.1 for Windows*. SAS Institute Inc., Cary, NC.
- Sumberg, J. and Gilbert, E. 1992. Agricultural mechanisation in The Gambia: draught, donkeys and minimum tillage. *African Livestock Research* 1: 1-10.
- Verstegen, M. W. A., Zwart, D., Hel, W. van der, Brouwer, B. O. and Wensing, T. 1991. Effect of *Trypanosoma vivax* infection on energy and nitrogen metabolism of West African dwarf goats. *Journal of Animal Science* 69: 1667-1677.
- Zwart, D., Brouwer, B. O., Hel, W. van der, Akker, H. N. van den and Verstegen, M. W. A. 1991. Effect of *Trypanosoma vivax* infection on body temperature, feed intake, and metabolic rate of West African dwarf goats. *Journal of Animal Science* 69: 3780-3788.

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