ELSEVIER

Veterinary Parasitology 85 (1999) 25–41

veterinary parasitology

The susceptibility of Djallonké and Djallonké-Sahelian crossbred sheep to *Trypanosoma congolense* and helminth infection under different diet levels

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Received 5 January 1999; accepted 25 March 1999

Abstract

Forty two Djallonké and 27 Djallonké-Sahelian crossbred sheep were compared during 34 weeks for their disease resistance and productivity in a multifactorial experiment including trypanosome infection, helminth infections and dietary level. Eight treatment combinations were formed in which the two breeds were balanced. Pyrexia was observed following trypanosome infection and was not different between the two breeds. However, a significant higher parasitaemia level, a shorter prepatent period and a lower antibody response in the crossbreds following infection, indicated a significant reduction of the trypanotolerance and confirmed the genetic origin of the trait. Neither helminth infection nor dietary level influenced the onset and level of parasitaemia or the level of antibody response following trypanosome infection. Trypanosome infection, helminth infection and low supplementary feeding caused independently significant reductions in PCV level and weight gain but these declines were not worse in crossbreds as compared to Djallonké. Independently, of the studied factors, crossbreds were generally heavier than Djallonké and also grew faster, especially during the second phase of the study. Crossbreds had significantly higher mean nematode egg output (epg) compared to Djallonké sheep but reduction of epg following deworming was similar in both breeds. The lower epg in the Djallonké breed indicated an innate resistance to helminths and/or more efficient immune response. Trypanosome infection tended to increase epg, confirming the immunosuppressive effect of the former. The higher body temperature in the Djallonké compared to crossbreds suggested a better heat tolerance in the former breed.

From this study it was concluded that Djallonké-Sahelian crossbred sheep inspite of a reduced trypanotolerance and lower resistance to helminth infection, posses a higher potential to intensify mutton production as compared to the pure Djallonké. However, appropriate measures should be taken to limit disease and stress factors in order to optimise production environment for this crossbred sheep.

Keywords: *Trypanosoma congolense*; Sheep – Protozoa; Feeding and nutrition; Djallonké-Sahelian sheep

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0304-4017/99/$ – see front matter
PII: S0304-4017(99)00087-4

1. Introduction

The fast growing human population and urbanisation in Africa stresses the need for boosting animal production. Trypanosomosis is still a major constraint for animal production in sub-Saharan Africa. Apart from attempts to reduce the vector and the use of trypanocidal drugs with the risk of inducing environmental pollution and drug resistance, the use of trypanotolerant livestock has been promoted as a more economic and justified way of combatting trypanosomosis. Trypanotolerance has been defined as the ability of certain breeds of ruminants to survive and remain productive in tsetse infested areas without the aid of chemotherapy (Chandler, 1952, 1958; Mortelmans and Kageruka, 1976; Murray et al., 1982). The origin of this trait is still not completely clear but is multifactorial. Decades of natural selection and survival of the fittest may have played an important role in appearance of trypanotolerance (Dolan, 1987). In West Africa, trypanotolerance is related to some breeds of taurine cattle (*Bos taurus*), which are humpless and of smaller size (Chandler, 1952). The mechanism of trypanotolerance in these cattle has been described as a control of anaemia and of the intensity and duration of parasitaemia (Dargie et al., 1979; Murray and Morrison, 1979). Although the N'Dama breed seem to remain productive under natural infection (Agyemang et al., 1992) they remain a very slow reproducer with high age at first calving, long calving intervals and low milk production. Efforts to increase individual production, including the production of crosses with more productive but trypanosusceptible cattle breeds such as Zebu type (*Bos indicus*), are leading to a higher demand on nutritional input and are often more susceptible to endemic diseases. In West Africa, the Djallonke sheep and West African Dwarf (WAD) goats are regarded as trypanotolerant (Mawuena, 1986; Osaer et al., 1994) although the WAD goats seem to be less tolerant than the Djallonke sheep when challenged with the same clone of *T. congolense* (Goossens et al., 1997a) or studied under natural tsetse challenge (Osaer et al., 1999).

Trypanotolerance in small ruminants has been described as an innate ability to remain productive under infection with very low mortality rather than to control the parasitaemia and anaemia (Osaer et al., 1994, 1997; Goossens et al., 1997a). Innate resistance in N'Dama cattle and Djallonké sheep has been proven by the fact that trypanotolerance is expressed already during primary infections (Paling et al., 1991a; Dwinger et al., 1992; Osaer et al., 1994). Due to their small size, Djallonké sheep are prejudged in The Gambia as less productive. Farmers therefore, have shown continuous and growing interest to import Sahel breeds because of their bigger size and expectation of better carcass yields. These trypanosusceptible Sahelian long-legged sheep are subclassified as Touabire or White Arab sheep from the North and Peul-Peul or Fulani from the central region in Senegal (FAO, 1991). The information available on comparing Djallonke and crossbred Djallonke-Sahelian sheep under different stress factors is very limited.

The main objective was to study disease resistance and productivity of Djallonké-Sahelian crossbred and pure Djallonké sheep. Therefore, both breeds were compared in a multifactorial design challenged with trypanosome infection, natural helminth infection and different diets. The responses of both breeds to trypanosome infection would in addition, further elucidate on the existence of a genetic base for trypanotolerance in the Djallonke breed.

2. Materials and methods

2.1. Site

The study was conducted on-station at the coastal site of the International Trypanotolerance Centre (ITC), The Gambia, West Africa. The climate is sub-humid with a mean annual rainfall of approximately 1000 mm. Based on entomological and pathological records, the site is generally considered to be at no risk of tsetse challenge (Rawlings et al., 1993).

2.2. Animals

Forty two pure Djallonké sheep and 27 F1-crosses (Djallonké × Sahelian sheep), either females or castrated males were selected from the ITC flocks following a breeding programme. Sahelian rams originating from northern Senegal were used for F1-crossbreeding after an adaptation period of 1 year. At the start, the experimental animals aged between 6 and 8 months. On average, the F1-crosses weighed 12.6 kg (σ 2.8) and the group of Djallonke's weighed 10.3 kg (σ 2.9) at the start of the experiment. All animals had been raised in absence of trypanosomosis risk, so the possibility of acquired resistance was non-existent. Within sex, animals were divided into blocks according to their age, followed by random allocation to eight different treatments. Assignment to groups was done separately for the two breeds to allow breed comparison. In this way, the number of Djallonke and F1-crosses present per group was balanced according to numbers available. All animals were vaccinated against Peste des Petits Ruminants (PPR-Tissue Culture Rinderpest vaccine, ISRA/LNRV, Dakar) which was repeated every 6 months. They were treated with pour-on acaricide against external parasites (Bayer, Bayticol® 1% pour-on, Flumethrin 1% at recommended dosage) and this was repeated every 4 weeks during the wet season. Prior to trypanosome infection the animals were checked for trypanosomes following examination of the buffy coat by dark ground (DG) microscopy (Murray et al., 1977) and serum was screened for antibodies against *T. congolense*, *T. vivax* and *T. brucei* by the Immunofluorescence Antibody Test (IFAT) (Katende et al., 1987).

2.3. Experimental design and sampling methods

The study started during the rainy season of 1997 (July) and had a total duration of 34 weeks. The design included the factors trypanosome infection (Tc or control), nutritional level (high or low) and natural helminth infection (Deworming or not D), resulting in eight different treatment combinations: 1 (Tc-H-Dew), 2 (C-H-Dew), 3 (Tc-H-nD), 4 (C-H-nD), 5 (Tc-L-Dew), 6 (C-L-Dew), 7 (Tc-L-nD), 8 (C-L-nD). In addition, a breed comparison was possible since the two breeds were allocated separately to treatment groups. Considering this design, 36 trypanosome-infected sheep could be compared with 33 controls, whereby all other effects are corrected for in the analyses. In a similar way, 36 high supplemented versus 33 low supplemented, 39 dewormed sheep versus 30 not treated sheep and 42 Djallonke versus 27 crossbreds were compared. Whether breeds responded differently to one of the above factors, was measured by the interaction breed and each of these factors.

A West African stock of *T. congolense* originating from a clone (SAT86/CRTA/91) from Burkina Faso was used as artificial infection. The stabilate was first expanded in a goat and thereafter the sheep assigned to infection groups (1, 3, 5 and 7) each infected intravenously with 1 ml of infected blood containing 10^5 trypanosomes. Infection took place on 17 July 1997 (Day 0) and all weeks refer to time post *T. congolense* infection. Trypanosome infection was terminated by treatment of all infected animals with trypanocidal drugs (Diminazene aceturate at 3.5 mg/kg bodyweight) at the end of Week 21. The dewormed groups (1, 2, 5 and 6) were given fenbendazole at strategic intervals during the rainy season – end July (Week 2), mid September (Week 9) and end October (Week 16) at the recommended dosage (Panacur®, 10%, Hoechst, Germany, 5 mg/kg bodyweight). The low nutrition groups (5–8) received a restricted supplement based on cotton seed, while the high nutrition groups (1–4) received a supplement based on groundnut cake, cotton seed and rice bran. The low level supplement offered about 40.5% of the required rumen degradable protein (RDP) and 20.7% of metabolisable energy (ME), based on a daily live-weight gain of 50 g/day. The highly supplemented groups received at least five times more to satisfy their demand for growth (Mcdonald et al., 1988). During daytime, all animals were grazing together on natural pastures to allow helminth infection and supplements were fed per group before grazing. Rectal temperatures were taken three times per week during the first 4 weeks. Animals were bled twice weekly between Week 0 and 3 and once weekly between Week 4 and 30. Packed cell volume (PCV) levels were assessed and parasitaemia was measured by the DG method and scored by the method of Paris et al. (1982). Serum was collected from the blood samples taken in Weeks 0, 4, 8 and 12 in order to measure the titre (1/dilution) of trypanosomal IFAT antibodies according to Magnus (1988) using Fluorescein-conjugated rabbit IgG fraction to sheep. Rectal faecal samples were collected from all animals at fortnightly intervals from Week 2 to 34. The number of strongyle eggs per gram faeces (epg) was determined using a McMaster technique with a sensitivity of 100 epg (Thienpont et al., 1979). Body weights were recorded weekly using a Salter Spring balance. After Week 22, all animals were further weighed fortnightly for another 3 months.

2.4. Statistical analyses

Statistical analyses were carried out using SAS (1998) statistical package version 6.12. Continuous parameters were analysed by the general linear model (GLM procedure) as repeated measurements using a mixed model. The model included the following main effects: infection (control versus infected), diet (low versus high), deworming (deworm versus not deworm), breed (Djallonké versus crossbred), sex, block (sex), period (acute: Week 0–5; post acute: Week 6–21; recovery: Week 22–34), week (nested within period), animal (nested within infection, diet, deworming, block, sex, breed, block) and their interactions (two-way, three-way and four-way). The interactions breed × infection, breed × diet, breed × deworming were of high interest in this study since they indicated whether breeds responded differently to the different factors. The other interactions gave evidence of interdependency of the studied factors. The animal effect was regarded as random. Parameters such as prepatent period and daily gain were analysed in a similar model but without the animal effect. Before analysis, egg output data (epg) were subjected to a logarithmic trans-

Table 1
Mortality in Djallonke and F1-crossbred sheep during a multifactorial experiment including trypanosomosis, helminthosis and high or low level of nutrition[a]

Group (total)	No died (breed)	Week	Symptoms	Post-mortem findings
1 Tc-H-Dew (10)	0	–		
2 C-H-Dew (11)	1 (Dj)	19	Respiratory problems, PCV 23	Fibrinous pleuropneumonia, hydropericard, petechial haemoraghes on pericard and endocard
3 Tc-H-nD (8)	0	–		
4 C-H-nD (7)	0	–		
5 Tc-L-Dew (11)	0	–		
6 C-L-Dew (7)	1 (Dj)	2	Lice infestation, weight loss, Diarrhoea, PCV 16	Mild hydrothorax, mild pneumonia
7 Tc-L-nD (7)	1 (Dj)	14	Treated-PCV < 15%	Survived
8 C-L-nD	1 (F1)	13	Weight loss, high epg, PCV 17	Generalised enteritis and inflamed lymphenodes
	1 (Dj)	18	Fever, PCV 28	Hydropericard, petechial haemoraghes on pericard and endocard, mild enteritis

[a] Absolute figures per group, indicate breed, week of death, clinical symptoms and post-mortem results.

formation to approximate a normal distribution. All hypotheses were tested by the *F*-test (Snedecor and Cochran, 1980). Results were regarded as statistically significant when the Type I error probability was smaller than 5%. Means of the different groups are presented as least square means ± standard error (s.e.).

3. Results

3.1. Clinical symptoms

During the observation period four animals died and one sheep needed trypanocidal treatment since its PCV level went below 15% and was consequently withdrawn from the trial. Table 1 gives an overview of groups and numbers died with symptoms and post-mortem observations. Three Djallonke and one F1 sheep died and all four originated from the youngest age blocks at the start of the experiment. All had a history of weakness and a decrease in PCV, however not below 15% and/or showed weight loss and high faecal egg counts. In one case, cowdriosis was suspected (Group 8) however, not confirmed by brain smear.

Following trypanosome infection, rectal temperature significantly increased ($P < 0.001$), with means of $39.56 \pm 0.03^{\circ}$C for infected groups versus $39.35 \pm 0.02^{\circ}$C for control groups. There was a breed effect ($P < 0.05$) with Djallonke sheep having a mean higher rectal temperature ($39.52 \pm 0.03^{\circ}$C) than crossbreds ($39.40 \pm 0.04^{\circ}$C). The interaction infection × breed was non significant (n.s.) indicating that both effects were additive and that two breeds were not responding differently to the trypanosome infection. Neither diet nor deworming had an effect on rectal temperature and also the interactions diet × infection and deworming × infection were not significant. There was an important variation between animals ($P < 0.001$).

3.2. Parasitaemia level and prepatent period

In all trypanosome infected animals (Groups 1, 3, 5, 7) the onset of parasitaemia or prepatent period was on average 8.8 ± 1.7 days. A longer prepatent period ($P < 0.05$) was observed in Djallonké sheep (9.4 ± 0.4 days) compared to the crossbreds (8.1 ± 0.5 days). All trypanosome infected groups had their first parasitaemic peak around Week 3 and showed subsequently a similar pattern up to trypanocidal treatment at the end of Week 21 (Fig. 1(a)). During the period of infection, crossbreds had higher parasitaemia levels ($P < 0.001$) than Djallonke sheep (score: 2.2 ± 0.1 versus 1.5 ± 0.1, respectively) (Fig. 1(b)). In non-trypanosome infected animals, no parasites were detected during the total duration of the experiment. Diet did not influence significantly the prepatent period, despite a tendency to be shorter in the low supplemented groups (8.3 days for low versus 9.1 days for high diet, pooled s.e. = 0.5). Neither the level of diet nor the deworming, influenced the parasitaemia level and none of the interactions were significant.

3.3. Packed cell volume

Mean weekly group PCV levels are presented in Fig. 2. Concurrently with the appearance of trypanosomes, PCV levels dropped ($P < 0.001$) due to infection (means of $22.5 \pm 0.1\%$ in infected groups versus $25.2 \pm 0.2\%$ in control groups). The interaction period × infection ($P < 0.001$) confirmed an important drop in PCV of $1.7 \pm 0.2\%$ due to infection between acute and post-acute phase. Low supplementary feeding also decreased PCV levels ($P < 0.001$), with overall means of $24.9 \pm 0.1\%$ and $22.8 \pm 0.2\%$ for high and low level diet groups, respectively. The groups receiving higher dietary supplements did not encounter the drop induced by infection, but both effects were acting independently since the interaction diet × infection was non-significant. Deworming had a positive effect on PCV (dewormed $24.7 \pm 0.1\%$ and not dewormed $23.0 \pm 0.2\%$) which was most apparent in the subacute phase (interaction period × dewormed; $P < 0.001$). Between breeds, there was no significant difference in PCV level. Crossbreds did not respond differently in terms of PCV changes to the trypanosome infection, diet or deworming compared to Djallonké sheep. In addition, there were no significant interactions between infection, diet and deworming, thus all effects were additional. This was clearly demonstrated by the lowest PCV levels in Group 7 (Tc-Nd-L) (Fig. 2).

3.4. Antibody response

Following trypanosome infection, titres of trypanosomal IFAT antibodies (1/dilution) were measured in the infected groups up to 90 days post infection. Neither supplementary feeding nor deworming, influenced the antibody level significantly despite an initial higher titre for the low supplemented groups (Fig. 3(a)). However, there was a significant breed difference ($P < 0.001$) with consistently lower levels for the crossbreds during the 3 months post infection and a mean titre of 652 ± 140 (1/dilution) in crossbreds versus 1476 ± 105 (1/dilution) in Djallonké sheep (Fig. 3(b)).

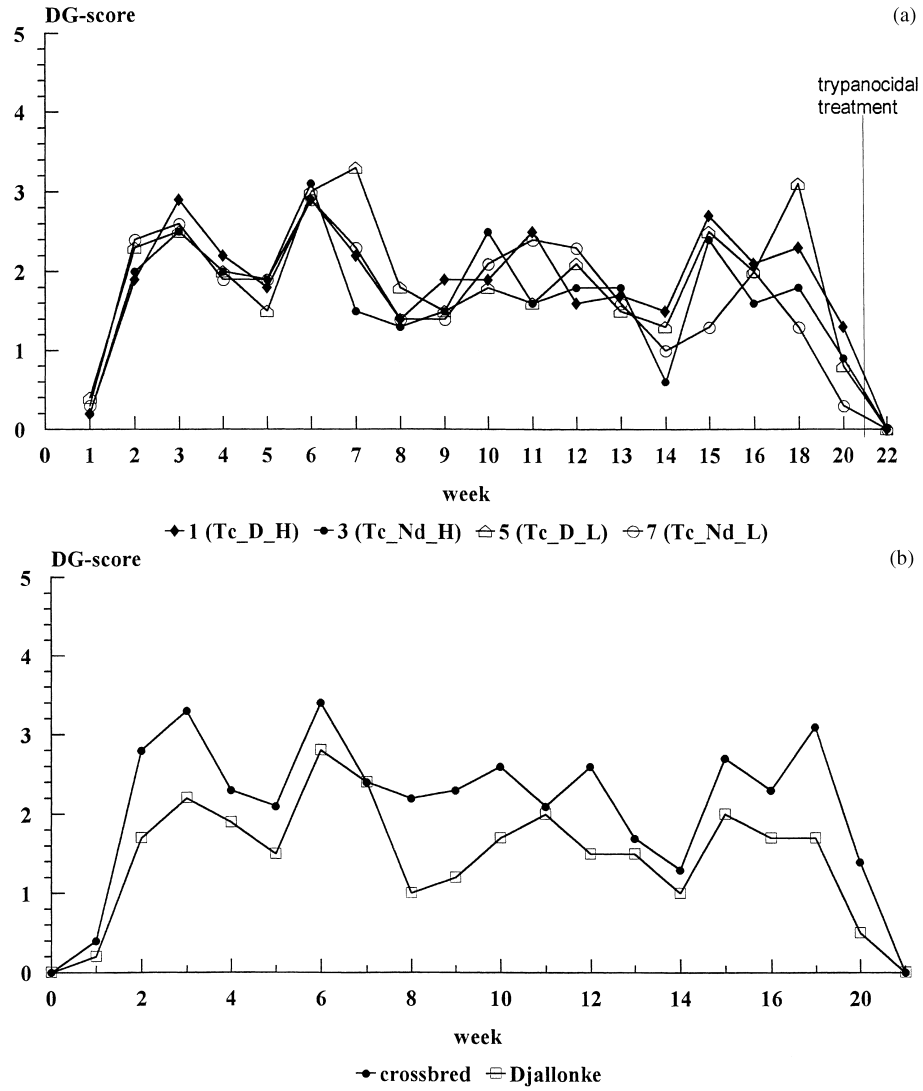

Fig. 1. (a) Parasitaemia levels of trypanosome infected sheep (comparison of four trypanosome infected groups under high or low level of nutritional supplementation and treated or not against helminths); (b) Parasitaemia levels of trypanosome infected sheep (comparsion of pure Djallonke sheep and F1-crosses with Sahelian breed).

3.5. Live weight

Mean weekly body weights are presented in Fig. 4. Trypanosome infection caused a reduction in weight gain of 0.7 kg ± 0.2 from the start till the end of the infection period (infection × period; $P < 0.01$) compared to the controls. However, over the entire study period, the difference in total weight gain between controls and infected groups was 1.6 kg ± 0.2

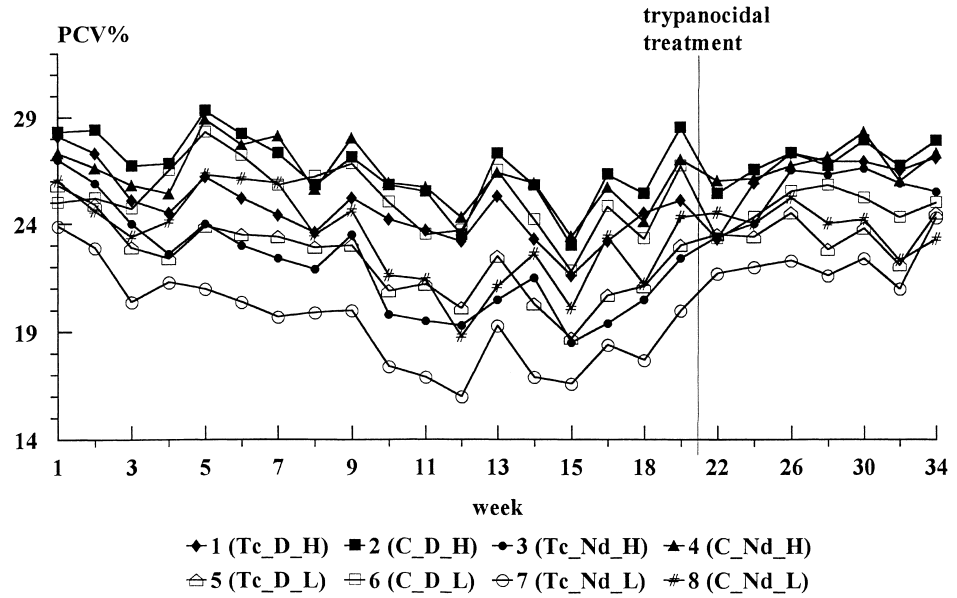

Fig. 2. Mean weekly packed cell volume % (PCV%) in sheep (comparison of eight groups infected with *Trypanosoma congolense* or controls, under high or low level of nutritional supplementation and treated or not against helminths); trypanocidal treatment in Week 21 post-infection.

Table 2
Effect of breed on individual daily weight gain (lsmeans ± s.e.; in g/day) during the period of infection and recovery: comparison between Djallonké sheep and F1-crossbreds (Djallonké × Sahelian)

Breed	Infection period (g/day)	Recovery period (g/day)
Djallonké	23.6 ± 2.4	44.5 ± 3.4
Crossbreds	27.6 ± 3.1	57.9 ± 4.3
Significance	n.s.	$P < 0.001$

($P < 0.001$). Dewormed animals had on average 1.1 kg ± 0.1 better weight gain compared to not-dewormed animals over the whole observation period (deworming × period; $P < 0.001$). High level of supplementary feeding caused a surplus in weight increase of 3.01 kg ± 0.2 compared to the low level (period × diet; $P < 0.001$). There were no significant interactions between trypanosome infection, diet or deworming, thus all effects were acting additive as is demonstrated by Group 7 (Tc-Nd-L) which had the lowest weight increase (Fig. 4). Although the two breeds differed in body weight ($P < 0.001$), the crossbreds did not respond differently in terms of weight changes than Djallonké sheep following trypanosome infection, diet or deworming. To compare growth rates between breeds, an individual daily weight gain (linear regression, $Y = b_0 + b_1$ days) was calculated for the period of infection and recovery, respectively and the estimated regression coefficient (b_1) was analysed in a similar model. During the period of infection (acute and post-acute phase), breeds did not show significantly different growth rates, whereas during the recovery phase, crossbreds had higher ($P < 0.001$) weight gains than Djallonké sheep (Table 2).

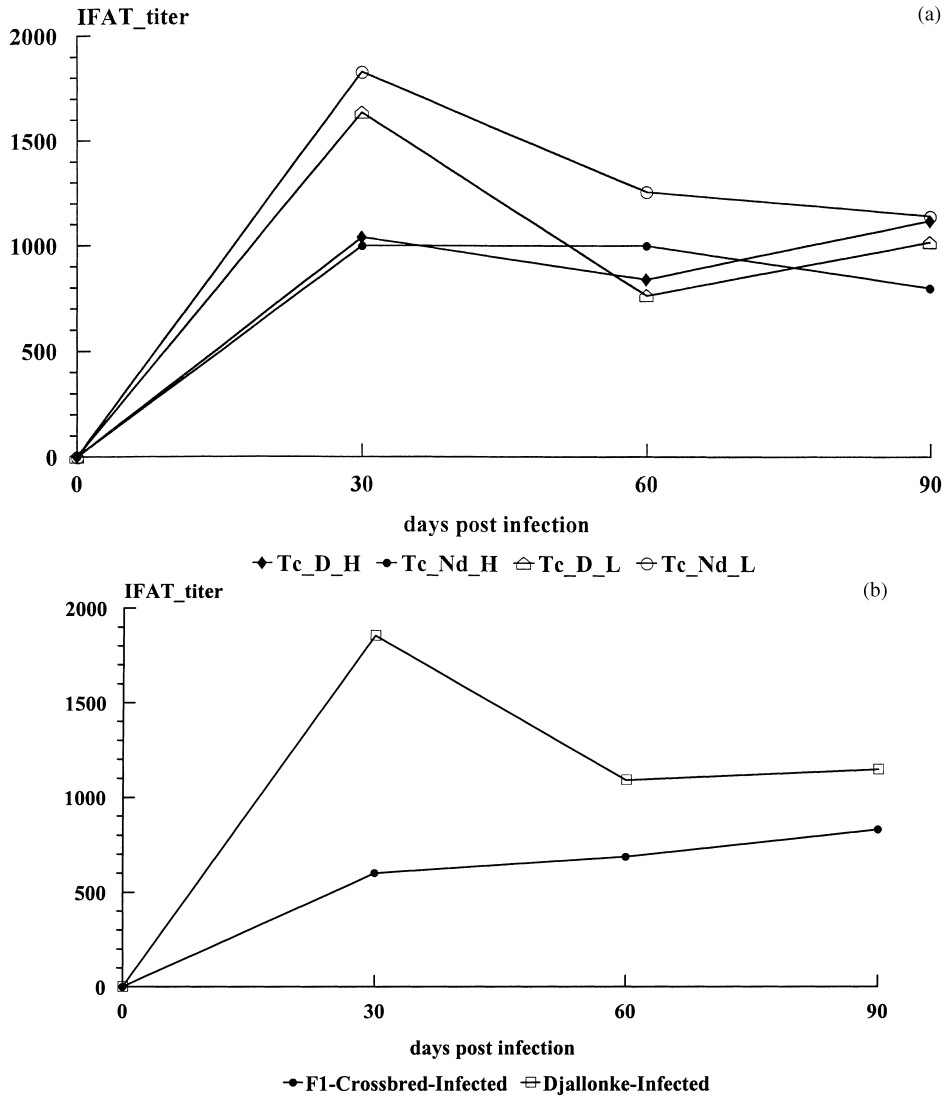

Fig. 3. (a) Mean antibody titers (IFAT) for sheep. Comparison of four groups infected with *Trypanosoma congolense*; (b) Mean antibody titers (IFAT) in sheep (comparison of Djallonke sheep with F1-crosses, with Sahelian sheep infected with *Trypanosoma congolense*).

3.6. Nematode egg excretion

The arithmetic mean weekly numbers of strongyle eggs per gram faeces (epg) are presented in Fig. 5(a). Peak egg excretion was seen for the not-dewormed groups (3, 4, 7 and 8) between Week 10 and 14, which corresponds to the period – end September–mid-October. Group 7 (Tc-Nd-L) and to a lesser extent Group 8 (C-Nd-L) had a second peak in Week 18.

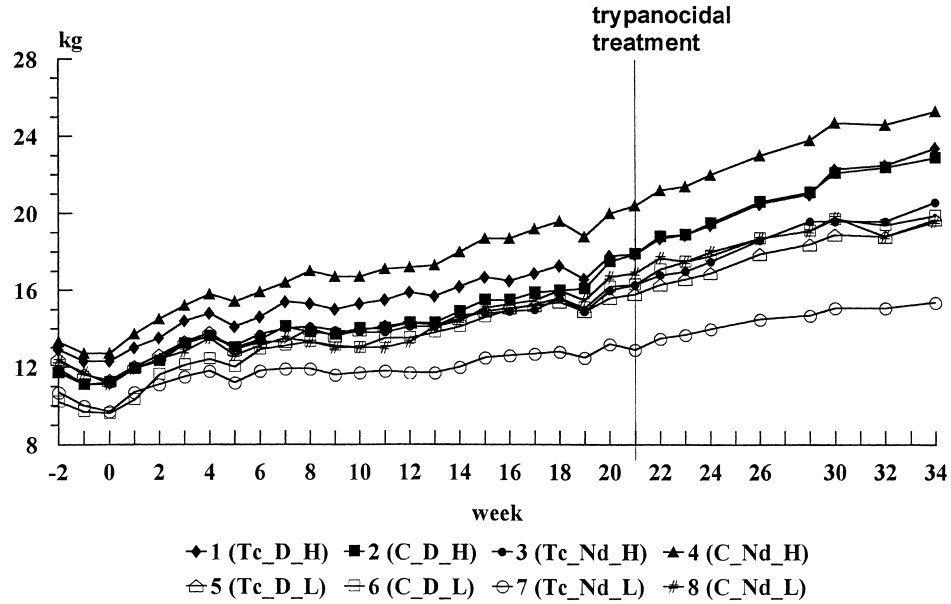

Fig. 4. Mean body weight changes in sheep (comparison of eight groups infected with *Trypanosoma congolense* or not, under high or low level of nutritional supplementation and treated or not against helminths); trypanocidal treatment in Week 21 post-infection.

Epg was significantly decreased by deworming ($P < 0.001$), with a difference in mean epg (log-transformed) of 1.94 between treated and not-treated animals for the period between Week 6 and 21. There was a significantly higher ($P < 0.01$) mean epg for the crossbreds (3.77 ± 0.15) compared to Djallonke (3.30 ± 0.13), illustrated also by the weekly arithmetic means of both breeds (Fig. 5(b)). However, crossbreds did not respond differently to the effects of deworming on epg. Diet had no effect on epg and also did not interact with the deworming. Trypanosome-infected groups tend to have higher epg levels with 3.67 ± 0.21 for infected groups versus 3.41 ± 0.15 for control groups, but the difference was not significant and there was no interference with the deworming effect (interaction; n.s.).

4. Discussion

Primarily, this experiment aimed at evaluating the resistance to the effects of a trypanosome infection in trypanotolerant sheep under basic dietary conditions challenged concomitantly with helminths. A second aim was to make a comparison between trypanotolerant sheep and their crossbreds with trypanosusceptible breeds to further elucidate a genetic basis for trypanotolerance in the former breed.

4.1. Mortality and clinical symptoms

Both Djallonké and crossbred sheep suffered from anaemia and weight losses as a result of trypanosome infection, helminths and low nutrition but mortality due to trypanosomosis

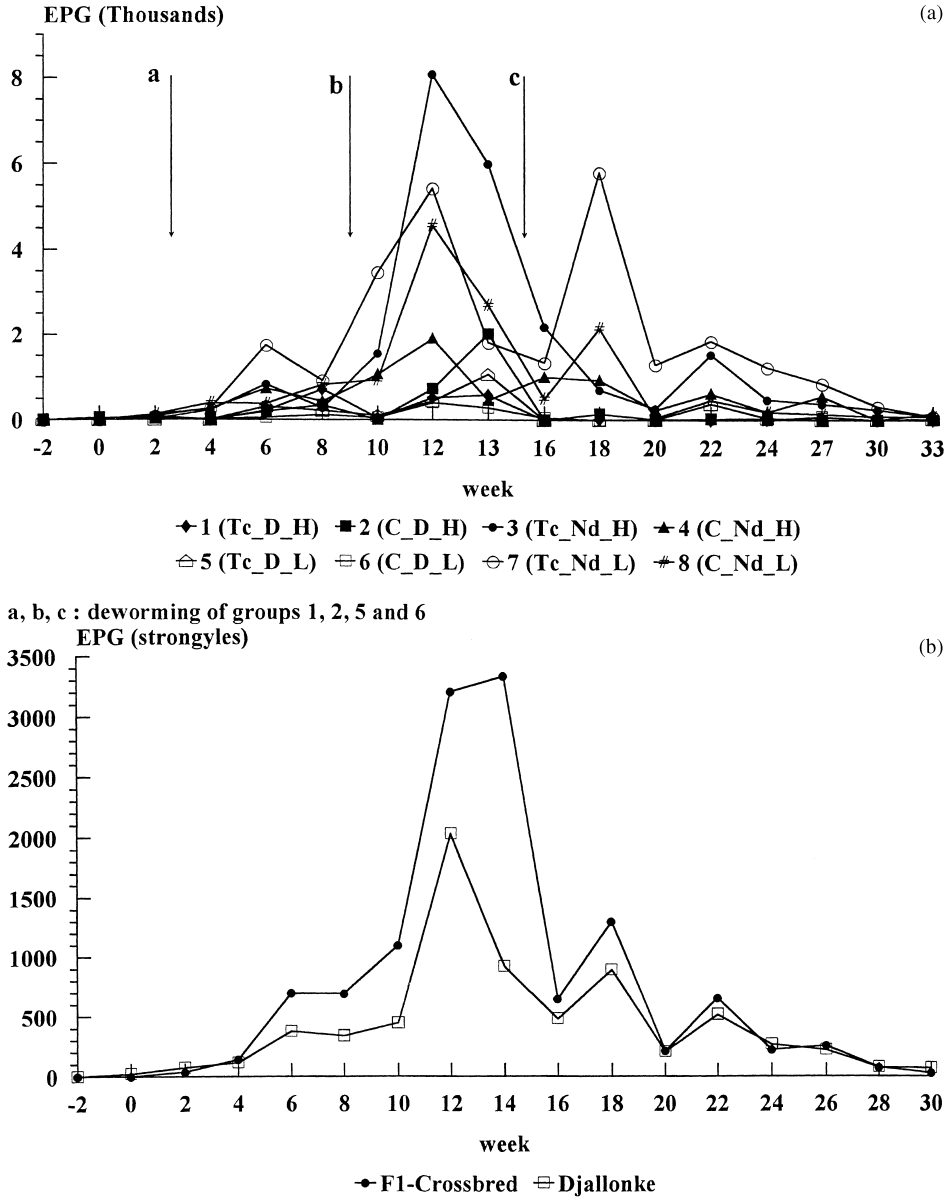

Fig. 5. (a) Mean faecal egg counts (epg) in sheep (comparison of eight groups infected with *Trypanosoma congolense* or not, under high or low level of nutritional supplementation and treated or not against helminths); (b) Mean faecal egg counts (epg) in sheep (comparison Djallonke sheep with F1-crosses with Sahelian sheep).

alone was non-existent. The sheep which died, originated from the blocks with younger age and lowest weight at the start and were kept under low nutritional conditions. The three Djallonke sheep which died, belonged to non-trypanosome infected groups and two were dewormed. Post-mortem findings gave suspicion of infection with *Cowdria ruminantium*, although this could not be confirmed by a positive brain smear. The one Djallonké sheep with PCV below 15% which was given trypanocidal treatment also originated from the block of youngest age, was not dewormed and fed low supplements. The two sheep from Group 8 (C-L-nD) which died were the youngest animals. In the F1-crossbred animal, mortality was clearly associated with clinical helminthosis, whereas for the Djallonke there was suspicion of cowdriosis. It has to be noted that the experimental animals did not have an acquired immunity since they were born during the previous dry season and this was their first contact with helminths. It was suggested earlier that acquired resistance in sheep under these climatic conditions was very low or non-existent (Ankers et al., 1994). Lambs up to 6 months of age were less able to mount a vigorous immune response or acquire protective immunity to helminth infection than older sheep (Lloyd and Soulsby, 1987). Due to the low mortality rates in general, no breed differences could be identified based on these results.

Pyrexia induced by the trypanosome infection during the first 4 weeks confirms the pathogenicity of the clone and is an important factor in the non-specific defence mechanism of the host (Kluger and Rothenburg, 1980). Pyrexia is associated with the peaks of parasitaemia waves during trypanosome infection (Losos and Ikede, 1972; Griffin and Allonby, 1979; Bengaly et al., 1993; Osaer et al., 1997; Goossens et al., 1997b). The higher body temperature found in Djallonké compared to crosses with Sahelian breeds might be due to better thermoregulatory abilities of the former. Heat tolerance, reported in trypanotolerant N'Dama cattle (Greig and Mcintyre, 1979) has also been observed in Djallonké sheep in Gambia (Osaer, unpublished observations). Another contributing factor could be the lower body weights exposed to the same environmental temperatures resulting in higher body temperatures, as was observed in Angora goats (Mcgregor, 1985).

4.2. Trypanotolerance

The onset of parasitaemia was delayed in Djallonké as compared to the F1-crosses. Since trypanosomes were inoculated intravenously, no localised skin reaction or chancre influenced the first appearance of parasites as observed in cattle (Murray et al., 1981). The difference in prepatent period between breeds could therefore only be due to differences in rapidity of humoral immune response. The intensity of parasitaemia was also consistently lower in the Djallonké sheep indicating that, even following primary challenge, they are capable to limit parasite multiplication better than crossbreds. Better control of parasitaemia level in trypanotolerant breeds has been shown in comparative studies with more susceptible cattle breeds (Roberts and Gray, 1973; Pinder et al., 1984, 1988; Paling et al., 1991a, b; Dwinger et al., 1992) or susceptible sheep breeds (Toure et al., 1981; Bengaly et al., 1993). One of the underlying mechanisms for better control of the parasitaemia is a superior immune response of the trypanotolerant breeds, feature mainly studied in cattle (Murray et al., 1982; Roelants and Pinder, 1984; Authié, 1994). Pinder et al. (1988) demonstrated an

earlier appearance and a higher titre of neutralising antibodies in more tolerant breeds. In the present study, control of parasitaemia and the humoral immune response in general was significantly reduced in the crossbreds as compared to pure Djallonke. The significantly higher level of antibodies in the Djallonke sheep during the first 3 months of infection, explains the consistently lower level of parasitaemia and confirms the superior immune response in this trypanotolerant breed. Despite a better immune response resulting in a controlled parasitaemia, there was no tendency for self-cure as described in trypanotolerant cattle following primary infection (Wellde et al., 1981; Nantulya et al., 1986). Self-cure in Djallonke sheep following a primary infection with *T. congolense* was observed only after 24 months (Goossens et al., 1997a). Self-cure may occur when the antigenic repertoire of that particular serodeme is exhausted (Nantulya et al., 1986). The difference with trypanotolerant cattle is that this process lasts apparently much longer in sheep. Dietary supplementation did not influence the onset or intensity of parasitaemia in the present trial which accords with previous findings (Katunguka-rwakishaya et al., 1995; Wassink et al., 1997). Groups with concurrently higher worm burdens did not express higher parasitaemia levels, indicating there was no immunodepressive effect caused by helminths.

The anaemia induced by trypanosome infection was similar in both breeds. This is in contrast with previous comparative studies when Djallonké are compared with pure Sahelian (Peulh) sheep (Toure et al., 1981). Also trypanotolerant-cattle breeds develop a less severe anaemia following trypanosome infection when compared with susceptible breeds and this anaemia was used as parameter to measure trypanotolerance (Dargie et al., 1979; Murray et al., 1981; Paling et al., 1991b; Dwinger et al., 1992). Trypanotolerant-sheep differ in that respect from cattle because they do not control the drop in haematocrit to the same extent. A better parameter to measure trypanotolerance in sheep is their potential to remain productive under trypanosome challenge (Osaer et al., 1994; Goossens et al., 1997a). Although, higher supplementation increased the level of haematocrit, it could not alter the drop, induced by infection. So, effects of diet and infection were adding up as reported elsewhere (Wassink et al., 1997). Non-dewormed groups had reduced PCV levels. Diet did not alter the effects of helminths on PCV, neither did the trypanosome infection, thus all effects were additive.

4.3. Liveweight gain

Trypanosome infection depressed live weight gain as demonstrated previously in Djallonké sheep under experimental infection (Osaer et al., 1997, 1999) and under natural challenge (Osaer, unpublished results). Earlier work reported on a transient reduction of feed intake and increased maintenance requirements due to infection all resulting in a reduced weight gain (Holmes, 1987; Verstegen et al., 1991; Akinbamijo et al., 1994; Osaer et al., 1999). The weight loss induced by infection was neither altered by dietary supplements nor deworming and was also not worse in crossbreds. Crossbreds are of a larger size, thus breed differences for body weight are obvious. Daily growth rates were higher in the crosses, especially when animals aged over 12 months. However, pre-weaning daily weight gain of crossbreds versus Djallonké was not better and in addition mortality rates were much higher in crosses (43%) versus Djallonké (15%) (Osaer, unpublished results).

4.4. Resistance to helminth infections

This study was carried out during the rains and peak strongyle egg excretion occurred between mid-September and mid-October. The strongyle egg excretion (epg) was sufficiently reduced by the applied deworming scheme, despite the possibility of reinfection. A recent deworming trial carried out in sheep on farm, applying the same treatment scheme as in the present study, resulted in significantly increased growth rates in sheep of all age classes (Osaer, unpublished observations). Trypanosome-infected sheep tend to have increased epg in line with earlier observations by Goossens et al. (1997b) in Djallonké sheep and by Dwinger et al. (1994) in N'Dama cattle. The immunodepressive effect of a trypanosome infection (Mackenzie et al., 1975) may have contributed to a reduced resistance to a subsequent infection with helminths. Diet did not interact with the level of nematode egg excretion. Abbot et al. (1986a, b) observed that lambs on a low protein diet were less able to withstand the pathophysiological consequences of a single infection with *H. contortus*. The mortality in the one F1 animal in the present study was clearly associated with clinical helminthosis, aggravated by low dietary supplements but this was not the case for the one Djallonke sheep in the same group (Group 8) based on clinical symptoms and post-mortem findings. Resistance against gastrointestinal strongyles is based on a history of exposure, age of the host and genetics (Gamble and Zajac, 1992; Baker, 1995). The first two factors in this study where similar for both breeds which implies that only genetics can explain the observed low egg output. Faecal egg output is a repeatable and heritable trait which has been accepted as a quantitative method for selection on helminth resistance (Baker et al., 1992). The lower faecal egg excretion found in the Djallonké as compared to crosses could indicate a better resistance to helminths in the former breed. This study adds some evidence for helminth resistance in Djallonke sheep to the indications already available (Assoku, 1981; Baker, 1995; Goossens et al., 1997b).

5. Conclusions

The present study demonstrates that trypanosome infection, helminth infection and low dietary level cause a considerable reduction in PCV level and weight gain, however, not worse in crossbreds as compared to Djallonké. Some aspects of the trypanotolerant trait were significantly reduced in the crossbreds as shown by a higher parasitaemia level, a shorter prepatent period and a lower antibody response following infection. These observations confirm a genetic origin of the trypanotolerant trait. The higher nematode egg excretion in crossbreds as compared to pure Djallonke is an indicator of innate resistance to helminths and/or more efficient immune response in the latter breed. The higher rectal temperatures found in the Djallonke breed confirms the existence of heat tolerance, inherent to local breeds. It is also concluded that the larger size and better growth rates of crossbreds may result in a higher production potential compared to the purebred Djallonké. However, if crossbreds are to be used to intensify and increase meat production, appropriate husbandry and strict health care measures should be taken to limit stress factors and optimise the productivity.

Acknowledgements

We thank the technical staff of the Small Ruminants Unit at ITC for their valuable effort in collecting the data. We thank Prof Leo Dempfle for his help in the experimental design of this study and Dr Jutta Jaitner for her assistance in the statistical analysis. We gratefully acknowledge the financial support from the Belgian Administration for Development Co-operation to carry out this study. We thank Dr Maarten Eysker of the Faculty of Veterinary Medicine of Utrecht University for his useful comments on the manuscript.

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