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Trypanosome infections and tick infestations: susceptibility in N'Dama, Gobra zebu and Gobra × N'Dama crossbred cattle exposed to natural challenge and maintained under high and low surveillance of trypanosome infections

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Abstract

Susceptibility to trypanosome infections and tick infestations was assessed in 51 N'Dama, 48 Gobra zebu and 37 Gobra × N'Dama crossbred (F1) cattle exposed to field-tick infestations and natural high tsetse challenge over more than one year. From these cattle, 12 animals of each breed were randomly selected and examined parasitologically for trypanosome infections and packed cell volume (PCV) twice a week (high surveillance, group HS). In the remaining 100 cattle trypanosome infection and PCV were monitored monthly (low surveillance, group LS). Mortality rates were recorded in both groups. Tick infestation was quantified fortnightly from all animals in group HS and from four to seven randomly selected animals of each breed in group LS. In both HS and LS groups, trypanocidal drug treatment was administered to trypanosome positive animals with PCV equal to or less than 20% or when they showed clinical evidence (dullness, weight loss) of trypanosomosis. In both groups, N'Dama cattle exhibited a superior capacity to control trypanosome infections and

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limit tick burdens. Particularly, in group HS N'Dama cattle showed lower trypanosome infection rate, higher mean PCV value, lower requirement for trypanocide treatments and lower tick load than crossbred and Gobra cattle in the corresponding group ($P < 0.05$ or greater). This was also true in N'Damas in comparison with crossbreds in group LS. Unfortunately, the high mortality occurring in Gobra cattle in group LS did not allow within group comparative analysis between N'Dama, Gobra and crossbred cattle overall the study period. No death occurred in N'Dama cattle maintained under high surveillance of trypanosome infection, while approximately 8% of crossbreds and 50% of Gobras died of trypanosomosis. In group LS, all Gobra and more than 70% of crossbred cattle died. In this group, mortality in N'Dama was limited to less than 16%. In both groups, differences in mortality were significantly higher ($P < 0.01$) in Gobras than in N'Damas. Within breed, animals of the three breeds maintained under high surveillance of trypanosomal infection showed higher mean PCV values, lower tick burdens and required proportionally less trypanocide treatments than corresponding cattle in group LS. The infection rate in N'Dama under high surveillance was lower in comparison with N'Dama cattle in group LS. There was no significant difference in mortality between groups within the N'Dama breed. Conversely, mortality rates were lower in crossbred and Gobra in group HS than in respective cattle in group LS. It was concluded that cattle of the three breeds suffered from trypanosomosis and that trypanosome infections affected tick susceptibility. However, N'Dama showed a superior ability to limit both the pathological effects of trypanosomosis and the level of tick infestations. Therefore, considering the cost of labour and consumable equipment required for a high surveillance, use of multi-disease resistant N'Dama cattle is recommended for the low-input traditional African farming systems in areas where trypanosomosis, ticks and tick-borne diseases are constraints to livestock production. Additional comparative investigations are needed to assess the impact of high surveillance scheme of trypanosome infection in different production systems in trypanotolerant and trypanosusceptible cattle exposed to different gradients of tsetse challenge.

Keywords: N'Dama; Gobra; Crossbred; Trypanosomosis; Tick infestation; Susceptibility

1. Introduction

Tsetse-transmitted trypanosomosis together with tick infestations and related infections impair the economic efficiency of the livestock industry in sub-Saharan Africa (Fox et al., 1993; Jongejan and Uilenberg, 1994). In large parts of the sub-humid and humid West African regions tsetse flies and ticks co-exist. Consequently, cattle populations are submitted to multi-vector and associated parasite challenges.

Previous studies have shown that N'Dama (*Bos taurus*) cattle have the capacity to limit the pathological effects of either experimental tsetse-induced (Paling et al., 1991a,b) or needle-imposed (Dwinger et al., 1992) trypanosome infections as they have under conditions of natural exposure (Murray et al., 1981). A degree of resistance to tick infestation has also been observed in the N'Dama breed (Mattioli et al., 1993; Koney et al., 1994).

In observations made on trypanosomosis in N'Dama and/or Gobra (*Bos indicus*) zebu cattle tick infestations were often controlled with chemicals (Dwinger et al., 1992; Trail et al., 1992) or not quantified (Murray et al., 1981). There is evidence that experimental *Trypanosoma congolense* infection increases susceptibility to *Rhipicephalus appendiculatus* infestation in rabbit (Heller-Haupt et al., 1983) and to tick-borne *Cowdria ruminantium* infection in trypanosusceptible Gobra zebu cattle (Mattioli et al., 1994). Conversely, Dossa et al. (1996) reported an enhanced ability to acquire resistance to *Amblyomma variegatum* in cattle infected with *T. congolense*. In these reports the role of the immune suppression caused by trypanosomosis (Darji et al., 1992) was debated. It is known that trypanocidal treatment reverses the immune suppression (Whitelaw et al., 1979). Restoration of immune response to normal is more rapid in animals receiving treatment in the early stage of infection than in those treated after long-standing trypanosome infection (Roelants et al., 1979).

The objective of the present study was, therefore, to investigate the susceptibility to trypanosomosis and to tick infestations in N'Dama, Gobra and Gobra × N'Dama crossbred cattle simultaneously exposed to tsetse and tick-field challenges. Two different surveillance schemes (high and low) of trypanosome infection were set up to explore their effects on susceptibility, parasitological and health traits within breed.

2. Materials and methods

2.1. Animals

A herd of 51 N'Dama (33 males and 18 females), 48 Gobra (35 males and 13 females) and 37 Gobra × N'Dama (F1) crossbred (24 males and 13 females) cattle was established in June 1995. Their ages ranged from 1.5 to 2.5 years. N'Dama and crossbred cattle were born and reared at the Kerr Serigne station of the International Trypanotolerance Centre (ITC), situated on the coast of Gambia. The tsetse challenge at the ITC site is zero (Dwinger et al., 1992). Gobra zebu cattle were from a tsetse-free area in northern Senegal (Dwinger et al., 1992). The Gobra cattle spent 2 months at the ITC Kerr Serigne station and were kept under the same management practices as N'Dama and crossbred cattle. In the first week of June 1995, i.e. 2 months prior to exposure of the animals to tsetse and tick-field challenges, jugular blood samples were collected from cattle and screened for the presence of trypanosomes by the buffy coat darkground-phase contrast microscopic technique (Murray et al., 1977). They were found negative. Animals also had no detectable anti-trypanosome antibodies or circulating trypanosomal antigens in collected serum samples, tested by immunofluorescence (Katende et al., 1987) and enzyme-linked immunosorbant assay based on species-specific monoclonal antibodies (Nantulya and Lindqvist, 1989), respectively. In July 1995, animals were dosed orally with an anthelmintic (albendazole, 7.5 mg/kg body weight (bw)), treated intramuscularly with a trypanocidal drug (diminazene aceturate, 7 mg/kg of bw) and

sprayed twice at fortnightly intervals with an acaricide (flumethrin, 0.6% solution). Cattle were also vaccinated against anthrax, black quarter and haemorrhagic septicaemia. No additional anthelmintic and acaricide treatments were provided to cattle during the study period.

2.2. Study site

In August 1995, animals were transferred to the Niamina East area (14° 58′W, 13° 51′N), 200 km from the Atlantic coast, within an 180° loop of the river Gambia.

The study area has seasonally high to moderate challenges of *Glossina morsitans submorsitans* Newstead and *G. palpalis gambiensis* Vanderplank, as estimated from trap catches (flies/trap/day) (Wacher et al., 1994). Vegetation is open Sudano–Guinean savannah woodland interspersed with ricefields and swamps towards the river (Rawlings et al., 1994). Climate in the study area is characterized by unimodal rainfall from July to October with a mean annual rainfall of 900 mm (Mattioli et al., 1997), followed by a cool early dry season from November to February and a hot late dry season from March to June.

The spectrum of natural-cattle tick fauna of the study site includes *Boophilus geigy*, *B. decoloratus*, *Hyalomma truncatum*, *H. marginatum rufipes*, *R. senegalensis* and *A. variegatum* (Mattioli et al., 1997). This tick fauna is similar to that of the region of origin of the Gobra cattle (Gueye et al., 1989).

2.3. Frequency of monitored traits in relation to animal groups

Packed cell volume (PCV) percentage was measured by micro-haematocrit centrifugation in blood samples collected from the jugular vein to quantify anaemia and the buffy coat was examined for trypanosomes (Murray et al., 1977). Twelve N'Dama, 12 crossbred and 12 Gobra cattle were randomly selected from the established herd. These cattle were monitored for haematocrit level and presence of trypanosomes every other day from August to October 1995 and twice a week during the remaining study period. They were designated as group HS (high surveillance). In the remaining animals PCV measurement and trypanosome detection were conducted at monthly intervals. These animals were classified as group LS (low surveillance). In both groups, animals with a PCV $\leq 20\%$ and found positive for trypanosomes or animals showing severe clinical condition associated with trypanosomosis (e.g. sensorial dullness, loss of appetite, emaciation), were treated with a trypanocidal drug (diminazene aceturate, 7 mg/kg of bw). If deaths occurred in group HS, the number of cattle of each breed in that group was maintained by replacing with animals of the same breed, sex and similar age from group LS. Data on mortality were recorded.

Tick collection was performed from September 1995 to October 1996. Adult ticks were collected fortnightly from the right side of the animal's body and the whole tail. Tick samples were preserved in 70% ethanol and identified in the laboratory. Ticks were collected from all cattle in group HS and, for comparative study within the breed, on four to seven cattle of each breed, according to the availability of animals, in group LS. Cattle were not treated with acaricide during the study.

2.4. Data preparation and statistical analysis

Data from the first month of tsetse exposure, i.e. August 1995, were excluded from the analysis, as stress due to transport can temporarily alter individual performance, including susceptibility to trypanosomosis (Dehoux, 1990). Thus, only data collected from September 1995 to October 1996 were used for analysis. Data collected from all experimental animals on a fixed day each month were employed for graphic presentation of seasonal variations in the proportion of cattle infected with trypanosomes and the seasonality of field-tick occurrence. Tick burdens reported refer to twice the number of half-body collection plus those ticks removed from the tail (Mattioli et al., 1997).

In order to evaluate the effect of the two trypanosomosis surveillance schemes on health, trypanosome infections, requirement for trypanocide treatments and tick infestations two levels of comparison were performed: between breeds of cattle belonging to the same group and between groups of animals of the same breed (within-breed comparison). Due to progressive deaths occurring in the Gobra breed, resulting in the absence of zebu cattle in group LS after February 1996, comparative analysis within the zebu breed was necessarily restricted to the period September 1995 to February 1996. The χ^2 test was used to compare mortality rates and number of trypanocidal treatments required. The proportions of treatments were calculated on the number of blood samples examined. Differences in numbers of trypanosome positive blood samples, levels of PCV and cumulative tick burdens were submitted to the analysis of variance (ANOVA). For traits tested with ANOVA, the statistical model included the factors breed, sex, group, date of sampling, animal (nested with breed) and the interaction between date of sampling and breed. The animal was regarded as random effect, while date of sampling and breed or group were regarded as fixed effects depending upon whether the comparison was performed between breeds or within breed, respectively. $P \leq 0.05$ was considered as statistically significant.

3. Results

3.1. Trypanosome positive blood samples, PCV levels and requirement for trypanocide treatments

Susceptibility to trypanosome infection in the three breeds was assessed by measuring number of trypanosome positive blood samples (Table 1), PCV levels (Table 2) and requirement for trypanocidal drug treatments (Table 3) in the three breeds.

Lower overall number of parasitaemic positive samples was detected in N'Dama in comparison with both crossbred ($F = 10.7$; $P < 0.001$) and Gobra ($F = 6.7$; $P < 0.02$) cattle in group HS. In that group also, N'Dama showed higher mean PCV level than crossbred ($F = 7.0$; $P < 0.02$) and Gobra ($F = 12.0$; $P < 0.001$) cattle. Conversely, there was no difference ($F = 0.2$; n.s.) between crossbred and

Table 1
Percentage of positive blood samples, as detected by BCT, in the three breeds in cattle in group LS and group HS (in parenthesis number of positive/number of blood samples examined)

Breed	Percentage of parasitaemic positive blood samples			
	September 1995-Feburary 1996		September 1995-October 1996	
	Group LS	Group HS	Group LS	Group HS
N'Dama	NC	NC	17.6[a] (85/505)	9.7[b]
F1	NC	NC	35.6[c](52/146)	14.9[d]
Gobra	44.8 (30/67)	20.8 (168/803)	NA	15.1[e] (217/1439)

NC, not considered; NA, not applicable; last gobra died in Feburary 1996.
Between breeds: [a] significantly different from [c] ($P<0.04$); [b] from [d] ($P<0.001$) and from [e] ($P<0.02$).
Within breed: [a] significantly different ($P<0.001$) from [b]; [c] versus [d] n.s.

Gobra cattle in the numbers of positive samples. In group LS, the number of parasitaemic positive samples was lower ($F=4.1$; $P<0.04$) and mean PCV level higher ($F=10.0$; $P<0.002$) in N'Dama than crossbred cattle. Within breed, N'Dama cattle in group HS showed a significant reduction ($F=33.5$; $P<0.001$) in the number of trypanosome-positive blood samples than corresponding animals in group LS. This tendency, although not significant ($F=1.4$; n.s.), was also observed in crossbred cattle. Conversely, in cattle in group HS haematocrit levels were higher both in N'Dama ($F=4.2$; $P<0.05$), as well as crossbreds ($F=7.9$; $P<0.006$) than in corresponding animals in group LS. This was also true in Gobra zebu ($F=56.2$; $P<0.001$) during the period September 1995 to Feburary 1996 (Tables 1 and 2).

All animals of the three breeds were found parasitaemic at least in one occasion before receiving a trypanocidal treatment (Table 3). On average, 34.7% (58/167) of all treatments in cattle in group LS was given to animals which were found aparasitaemic but showed clinical signs of trypanosomosis (30.3% (19/62) in

Table 2
Overall mean packed cell volume (PCV) percentage in the three breeds in cattle in group LS and group HS (n, number of blood samples examined)

Breed	Mean PCV $\pm$ S.E.			
	September 1995–Feburary 1996		September 1995–October 1996.	
	Group LS	Group HS	Group LS	Group HS
N'Dama	NC	NC	20.7 ± 0.1^{c} ($n=505$)	21.5 ± 0.1^{d} ($n=1560$)
F1	NC	NC	18.9 ± 0.3^{e} ($n=146$)	20.1 ± 0.1^{f} ($n=1560$)
Gobra	16.7 ± 0.5^{a} ($n=67$)	19.9 ± 0.1^{b} ($n=803$)	NA	20.4 ± 0.1^{g} ($n=1439$)

NC, not considered; NA, not applicable, last gobra died in Feburary 1996.
Between breeds: [c] significantly different ($P<0.002$) from [e]; [d] from [f] ($P<0.02$) and from [g] ($P<0.001$).
Within breed: [a] significantly different ($P<0.001$) from [b]: [c] from [d] ($P<0.05$); [e] from [f] ($P<0.006$).

Table 3
Trypanocidal drug treatements in the three breeds in cattle in group LS and group HS, as based on haematological findings or on clinical condition associated with trypanosomosis (in parentheses number of treatements on number of cattle examined for trypanosomosis)

Breed	Proportion of trypanocide treatements			
	September 1995–Feburary 1996		September 1995–October 1996.	
	Group LS	Group HS	Group LS	Group HS
N'Dama	NC	NC	12.3[c] (62/505)	2.7[d] (42/1560)
F1	NC	NC	39.7[e] (58/146)	8.4[f] (131/1560)
Gobra	70.1[a] (47/67)	10.3[b] (83/803)	NA	8.2[g] (118/1439)

NC, not considered; NA, not applicable; last gobra died in Feburary 1996.
Between breeds: [c] significantly different ($P<0.001$) from [e]; [d] from [f] ($P<0.001$) and from [g] ($P<0.001$).
Within breed: [a] significantly different ($P<0.001$) from [b]; [c] from [d] ($P<0.001$); [e] from [f] ($P<0.001$)

N'Damas, 39.7% (22/58) in crossbreds and 36.2% (17/47) in Gobras). The mean PCV values in these animals did not significantly differ from those of the same breed and group receiving treatment when parasitaemic (data not shown). In group HS, only three crossbreds (mean PCV 18.3) and two Gobras (mean PCV 17.0) were aparasitaemic when treated, while none of the N'Dama cattle found negative for trypanosome required treatment. Analysis of trypanocidal drug treatment required showed that within breed significantly higher overall number of infections required treatment in animals of the three breeds in group LS in comparison with corresponding cattle in group HS ($\chi^2 = 73.3$; $P < 0.001$ for N'Damas; $\chi^2 = 133.0$; $P < 0.001$ for crossbreds and $\chi^2 = 174.1$; $P < 0.001$ for Gobra zebus). Between breed comparison, conversely, in animals in group HS requirement for treatment was significantly lower in N'Dama than in crossbreds ($\chi^2 = 489.5$ $P < 0.001$) and Gobras ($\chi^2 = 45.0$; $P < 0.001$). There was no significant difference in number of treatments between Gobras and crossbreds ($\chi^2 = 0.04$; n.s.). In group LS, the number of treatments administered to crossbreds was significantly higher ($\chi^2 = 56.7$; $P < 0.001$) than that given to N'Damas (Table 3).

In all the three breeds, proportions of individual trypanosome species detected in positive blood samples were similar both in animals in group HS and in group LS, with a high predominance of *T. vivax* over *T. congolense* and *T.b. brucei* (Table 4). During the period of high tsetse challenge (September to December 1995), all animals of the three breeds experienced several trypanosome infections (Fig. 1). Subsequently, the number of animals found positive declined along with the decrease of tsetse challenge. At the onset of the hot dry season (March 1996) until mid rainy season (August 1996), a low proportion of animals was found trypanosome positive. In the following late rainy season 96, both tsetse challenge and trypanosome infection rate increased. Throughout the study period mean PCV levels remained low in all three breeds.

Table 4
Proportions of individual trypanosome species in the three breeds in cattle in group HS and group LS (percentages do not consider mixed infections; in parentheses number of parasitaemic blood samples)

Cattle breed	Cattle group	Proportion (%) of trypanosome species			Total
		T. vivax	*T. congolense*	*T.b. brucei*	
N'Dama	HS	90.4 (141)	9.6 (15)	0.0 (0)	100.0 (156)
	LS	92.0 (81)	8.0 (7)	0.0 (0)	100.0 (88)
F1	HS	86.4 (204)	11.4 (27)	2.2 (5)	100.0 (236)
	LS	83.0 (49)	11.9 (7)	5.1 (3)	100.0 (59)
Gobra	HS	89.5 (197)	8.2 (18)	2.3 (5)	100.0 (220)
	LS	86.0 (31)	14.0 (5)	0.0 (0)	100.0 (36)
Total		88.4 (703)	10.0 (79)	1.6 (13)	100.0 (795)

3.2. Mortality rate

During the study period, mortality in all three breeds was mainly concentrated in September to December 1995. This period coincided with high tsetse challenge and a high proportion of animals infected with trypanosomes (Fig. 1). Clinical signs combined with haematological findings, i.e. the presence of trypanosomes and a low

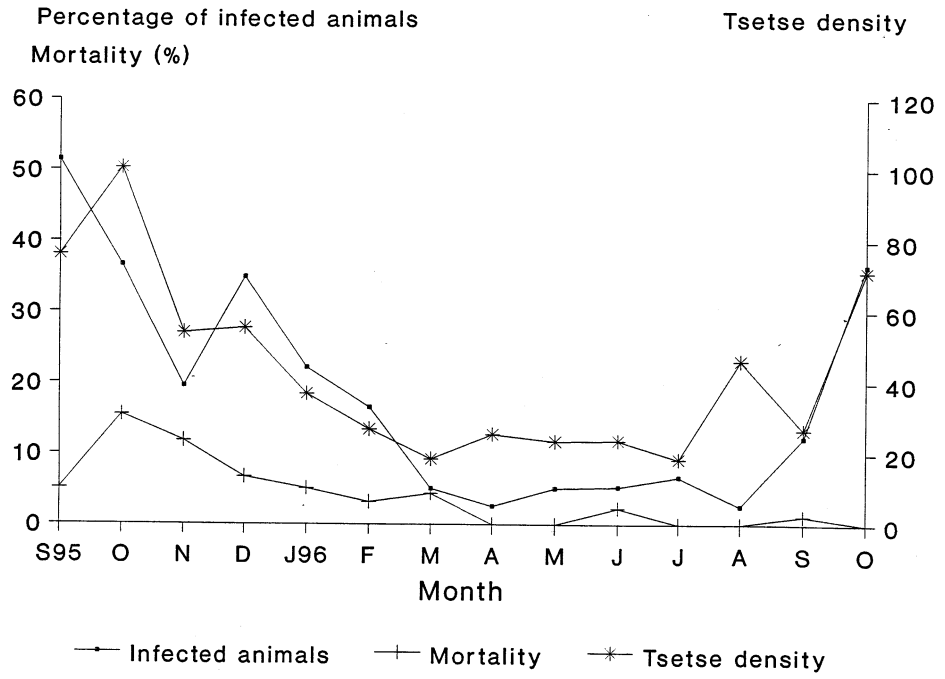

Fig. 1. Apparent tsetse density, as estimated from the number of catch/trap/day, percentage of animals infected with trypanosomes and mortality rate in all breeds from all groups during the study period.

Table 5
Overall mortality rates in the three breeds in cattle in group LS and group HS (in parentheses number of deaths/total number of animals at the start of the study)

Breed	Mortality rate (%)	
	Group LS	Group HS[a]
N'Dama	15.4[b] (6/39)	0.0[c] (0/12)
F1	70.8[d] (17/24)	7.7[e] (1/13)
Gobra	100.0[f] (31/31)	47.1[g] (8/17)

[a] If an animal died it was replaced with another animal from group LS.
Between breeds: [b] significantly different from [d] ($P<0.01$) and from [f] ($P<0.01$) [d] from [f] ($P<0.01$); group HS: [c] significantly different ($P<0.01$) from [g]; [e] from [g] ($P<0.05$).
Within breeds: [b] versus [c] n.s.; [d] significantly different ($P<0.01$) from [e]; [f] from [g] ($P<0.01$).

PCV value, and clinical condition observed in sick animals indicated trypanosomosis as the cause of deaths. No clinical condition associated with tick-borne anaplasmosis or babesiosis were observed.

Over the whole study period, in animals maintained under low trypanosomosis surveillance (group LS), mortality rate was significantly lower in N'Dama than in Gobra ($\chi^2 = 49.6$; $P < 0.01$) and their F1 crosses ($\chi^2 = 19.7$; $P < 0.01$) (Table 5). In this group, all the Gobra zebus died with the last death occurring in February 1996, i.e. 7 months after tsetse exposure. Mortality was also lower in crossbreds in comparison with that observed in Gobra zebu cattle ($\chi^2 = 10.3$; $P < 0.01$). In group HS no deaths occurred in N'Dama cattle. In this group also, mortality rate was higher in Gobra in comparison with both N'Dama and crossbred cattle (N'Dama versus Gobra, $\chi^2 = 7.8$; $P < 0.01$; crosses versus Gobra, $\chi^2 = 5.4$; $P < 0.05$). Within breed, significantly higher mortality occurred in Gobra ($\chi^2 = 19.1$; $P < 0.01$) and crossbred ($\chi^2 = 8.7$; $P < 0.01$) cattle in group LS than in corresponding animals in group HS, while there was no statistical difference ($\chi^2 = 0.6$; n.s.) between groups within the N'Dama breed (Table 5).

3.3. Tick burden

Of the total ticks collected from experimental animals ($n = 29691$), *B. geigy* was the most abundant ($n = 11040$; 37.2%), followed by *R. senegalensis* ($n = 8006$; 27.0%), *H. truncatum* ($n = 4604$; 15.5%), *H.m. rufipes* ($n = 3500$; 11.8%), *B.decoloratus* ($n = 2206$; 7.4%) and *A. variegatum* ($n = 335$; 1.1%). Tick mean counts (Fig. 2) were moderately high between October 1995 and January 1996 (42.1 ticks/animal), followed by a decline with mean counts remaining below 15 ticks/animal from February to October, except in April. The period of maximum tick infestation was characterized chronologically by the occurrence of *Hyalomma* spp. (September to January), *R. senegalensis* (October and November) and *Boophilus* spp. (October, December and January 1996). *A. variegatum* adults occurred in low number throughout the study period with a moderate increase in July and August 1996.

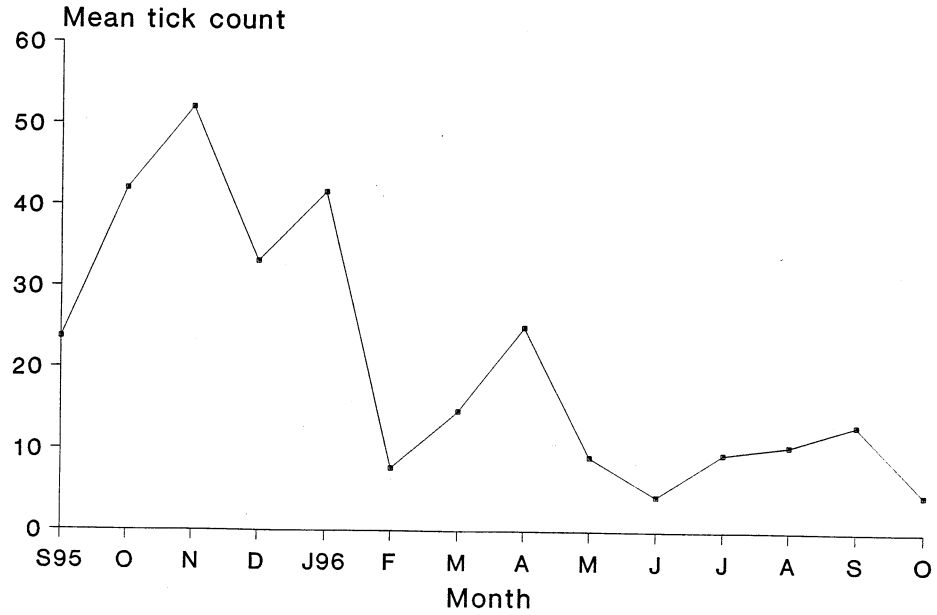

Fig. 2. Seasonal mean tick counts/animal in all breeds from all groups.

Within breed, overall mean tick burden was significantly lower both in N'Damas ($F = 4.3$; $P < 0.04$), crossbreds ($F = 8.2$; $P < 0.005$) and Gobras ($F = 10.2$; $P < 0.002$) in group HS than in corresponding animals in group LS (Table 6). However, between breeds comparison revealed that in group HS, N'Dama carried a significantly lower number of ticks than crossbred ($F = 7.7$; $P < 0.009$) and Gobra ($F = 5.3$; $P < 0.02$) cattle, but there was no difference ($F = 0.2$; n.s.) between crossbreds and Gobras. Similarly, in group LS, overall mean tick burden was significantly lower in N'Dama than in F1 ($F = 12.9$; $P < 0.001$) (Table 6).

Table 6
Mean cumulative tick burden in the three breeds in cattle in group LS and group HS (n, number of animals multiplied by the number of observations)

Breed	Tick Burden mean ± S.E.			
	September 1995–Feburary 1996		September 1995–October 1996.	
	Group LS	Group HS	Group LS	Group HS
N'Dama	NC	NC	20.1 ± 1.6^{c} ($n = 202$)	14.7 ± 0.9^{d} ($n = 333$)
F1	NC	NC	24.7 ± 2.8^{e} ($n = 135$)	22.3 ± 2.4^{f} ($n = 335$)
Gobra	54.2 ± 5.5^{a} ($n = 59$)	34.3 ± 2.7^{b} ($n = 143$)	NA	22.3 ± 1.5^{g} ($n = 302$)

NC, not considered; NA, not applicable; last gobra died in Feburary 1996.
Between breeds: [c] significantly different ($P < 0.001$) from [e];[d] from [f] ($P < 0.009$) and from [g] ($P < 0.02$).
Within breed: [a] significantly different ($P < 0.002$) from [b]; [c] from [d] ($P < 0.04$); [e] from [f] ($P < 0.05$).

treatment (Whitelaw et al., 1979; Masake et al., 1981). Re-establishment of the immune response occurred as early as 8 days after diminazene aceturate treatment with a positive correlation between duration of infection and time of recuperation after treatment (Roelants et al., 1979). In the present study, cattle of the three breeds in group HS carried significantly lower mean tick burdens (all species combined) than corresponding animals in group LS. This is probably related to a temporary restoration of a more effective immune response in animals maintained under a more timely treatment regime. Moreover, tick bite elicits a hypersensitivity skin reaction (Lloyd and Walker, 1993) which is effective in mediating host tick resistance (Walker and Fletcher, 1990) through the release of cellular derived histamine (Brown, 1985). Pain induced by histamine stimulates host grooming, a factor implicated in tick rejection (Bennet, 1969). Hypersensitivity skin reaction, observed in cattle infected with *T. congolense* and treated with diminazene aceturate, was not reported in cattle undergoing an active *T. congolense* infection (Emery et al., 1980). Furthermore, the degree of inhibition of skin reaction appears to be related to the duration of trypanosome infection, with profound suppression occurring after 5–6 weeks of infection (Murray et al., 1974). It may be possible that in animals in group LS suffering more from trypanosomosis, as assessed by their lower haematocrit levels, the grooming reflex could have been altered or attenuated leading to a higher tick attachment rate.

Dossa et al. (1996) reported enhanced resistance to artificially induced *A. variegatum* infestations, as assessed by adult tick feeding performance, in experimentally *T. congolense*-infected Boran zebu cattle. Another study showed that susceptibility to field infestations of *A. variegatum* and *Hyalomma* spp., as measured by the number of attached adult ticks during their respective period of abundance, was not affected in N'Dama cattle during the course of an experimental *T. congolense* infection (Mattioli et al., 1994). Conversely, our results suggest that repeated field-trypanosome infections could increase tick susceptibility in N'Dama and Gobra cattle. These contrasting findings might be explained by the different levels of *A. variegatum* and *Hyalomma* spp. that occurred during the previous and present trials over the respective study periods. Species-specific tick resistance is expressed above a certain threshold of that tick species density (Fivaz et al., 1992). However, caution should be taken in comparing results extrapolated from a single experimental trypanosome infection with those obtained in animals maintained under constant field-vector challenge.

It emerges from this study that trypanotolerant N'Dama cattle can also suffer from trypanosomosis under high tsetse challenge and that repeated trypanosome infections compromise resistance to ticks in all three cattle breeds. However, N'Dama showed a superior ability in comparison with Gobra and their crosses with N'Dama cattle to limit the deleterious consequences of trypanosome infections and the level of field-tick infestation.

It has been postulated that tick resistance can reduce the challenge rate of tick-borne pathogens through the reduced number of ticks attached onto animals (Fivaz et al., 1989; Mattioli et al., 1995). Moreover, it has been demonstrated that transmission of pathological agents is impaired in ticks attached onto resistant

animals (Francis and Little, 1964). It is concluded that the use of comparatively dually trypanotolerant and tick resistant cattle, such as the N'Dama breed, should therefore be encouraged in those areas where trypanosomosis, ticks and tick-borne diseases are constraints to livestock production. This will be particularly beneficial in the low-input traditional African farming systems (Itty, 1996) in which the regular surveillance of pathogens is lacking and the use of chemicals to limit the negative effects of pathogen agents for improved livestock production is limited by their relatively high cost. However, further studies need to be conducted to assess the impact associated with different surveillance schemes of trypanosome infection in different production systems in trypanotolerant and trypanosusceptible cattle submitted to various gradients of tsetse challenge.

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4. Discussion

Trypanosome infection in cattle usually causes anaemia followed eventually by death (Murray et al., 1981). Anaemia is more severe in long-standing infection (Murray and Dexter, 1988). In the present study, anaemia was less intense and/or mortality was lower in cattle of the three breeds more timely treated, i.e. animals in group HS, than in cattle maintained under low surveillance for trypanosomosis.

Both trypanotolerant and trypanosusceptible cattle appear to be equally susceptible in acquiring trypanosome infection following experimental tsetse bite (Paling et al., 1991a). When challenged, the immune system of N'Dama reacts more efficiently to a wider range of trypanosome antigenic stimuli than does the immune system of zebu cattle (Flynn et al., 1992), with deaths occurring in low immune-responder animals (Shapiro and Murray, 1982). In addition, the ability to control both parasitaemia and anaemia have been proposed as indicators for trypanotolerance (Murray et al., 1990). In the present study, all the animals were submitted to a continuous tsetse challenge and experienced several infections with different trypanosome species. Thus, besides the higher mortality observed in Gobra in both groups, tolerance to trypanosome infections in the N'Dama breed is further supported by the higher number of positive blood samples and lower mean PCV values found in crossbred animals in both groups, as well as in Gobra zebu cattle in group HS. These findings corroborate previous observations in different N'Dama and Gobra zebu populations in Gambia (Murray et al., 1981). Moreover, although lower than in group LS, the mortality rate in the Gobra breed was elevated even in group HS. Furthermore, requirement for trypanocidal drug treatment was lower in N'Dama than in crossbred and Gobra cattle. A similar situation was reported in N'Dama and Boran zebu cattle challenged with different tsetse-transmitted clones of *T. congolense* (Paling et al., 1991b). It has also to be considered that a certain degree of immunity develops in animals assisted by chemotherapy following a brief period of trypanosome infection (Wilson, 1971). Thus, it might be possible that cattle in group HS reacted more efficiently to local trypanosome infections and developed a superior ability to limit parasitaemia and the deleterious effects (anaemia, mortality) associated to trypanosomosis than animals in group LS. This might have contributed to lessen the requirement for trypanocidal treatments in animals in group HS in comparison to corresponding cattle in group LS. However, the observed scenario emphasises the importance, in field situations, of a stricter surveillance of trypanosomosis and timelier treatment in susceptible animals. Alternatively, it can be postulated that the trypanotolerant feature of the N'Dama breed might have allowed these cattle to limit the effects of concurrent pathogens, such as tick-transmitted *C. ruminantium* (Mattioli et al., 1994).

Immune depression induced by trypanosomosis is known to impair resistance to *R. appendiculatus* infestation in *T. congolense*-infected rabbits (Heller-Haupt et al., 1983). In cattle and mice, a significant level of immunosuppression appears after 7–8 days of trypanosome infection (Roelants et al., 1979; Masake et al., 1983; Flynn and Sileghem, 1991) and requires a constant presence of parasites in the bloodstream (Roelants et al., 1979). This phenomenon is reversed by trypanocidal