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Source: Journal of Wildlife Diseases, 11(1) : 68-75

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-11.1.68

THE ROLE OF WILD MAMMALS IN THE EPIDEMIOLOGY OF BOVINE THEILERIOSES IN EAST AFRICA*

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Abstract: The Theileriidae of East African wild mammals are reviewed.

Three species of wild Bovidae were captured in East Africa. They were African Cape buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*) and eland (*Taurotragus oryx*), and all were found to be naturally infected with *Theileria* species. These animals were studied to determine the transmissibility and pathogenicity of their theilerial infections to cattle. Adult *Rhipicephalus appendiculatus* ticks, which had engorged as nymphs on buffalo, transmitted fatal *Theileria lawrencei* infections to cattle. African buffalo were shown to be continually infective for ticks over a period of many months, demonstrating that buffalo can remain a carrier of *T. lawrencei*. In contrast, attempts to transmit the *Theileria* of wildebeest and eland to cattle through rhipicephalid ticks failed, despite the establishment of these parasites of the ticks. The significance of these results is discussed in relation to the epidemiology of bovine theilerioses.

During these studies, *Anaplasma marginale* was transmitted by blood passage from wildebeest to splenectomized calves.

INTRODUCTION

East Coast fever (ECF) is a highly pathogenic tick-borne disease, caused by the protozoan parasite *Theileria parva.*[35] It produces heavy losses in cattle in East Africa and, therefore, is a major restraint to improved livestock production in this region.[16] Methods of control of this and other bovine theilerioses are being investigated at the East African Veterinary Research Organization (EAVRO) in Kenya and, since theilerial parasites have been demonstrated in many species of wild mammals in East Africa,[11,27] part of the research program is directed towards studies on the role of these animals in the epidemiology of bovine theilerioses.

The objectives of this paper are threefold: to review previous work on theilerial and related infections of wild African mammals, to describe recent studies at EAVRO on the transmissibility and pathogenicity of these infections to cattle, and to discuss the significance of these results.

REVIEW

Theilerioses of Cattle

There are three species of *Theileria* that are known to be infective for cattle in East Africa. They are *T. parva, T. lawrencei*[30] and *T. mutans*,[36] and their behavior in cattle has been described in detail by Neitz.[27] *T. parva* and *T. lawrencei* are the causative organisms of two highly fatal tick-borne diseases of cattle, ECF and Corridor disease, respectively. *T. mutans* is considered to be nonpathogenic, but recently a strain pathogenic for cattle has been isolated in Kenya.[17]

* Paper presented at the 1974 Annual Wildlife Disease Conference at Asilomar, California.

Theilerioses of African Cape Buffalo

The African Cape buffalo (*Syncerus caffer*) has been shown to be susceptible to experimental *T. parva* infection,[1,21,27] but infected animals only underwent mild reactions. Adult *Rhipicephalus appendiculatus* ticks, fed as nymphs on two of these infected buffalo, transmitted fatal ECF to cattle.[1,21] However, isolation of classical *T. parva* direct from wild buffalo has not been reported.

A new theilerial syndrome of cattle, called Corridor disease, was described in 1955 from South Africa,[29] and African buffalo were found to be reservoirs of the infection. Neitz considered the causative agent of Corridor disease to be distinct from *T. parva,* since fatal infections in cattle involved only small numbers of macroschizonts, and mictoschizonts and intraerythrocytic piroplasms were rare or absent. These differences from *T. parva* led him to name the buffalo-derived parasite *T. lawrencei.*[28] *T. lawrencei* has been isolated from buffalo also in Kenya.[9] Fatal reactions to *T. lawrencei* infection have been reported in African buffalo,[9,27] but the case fatality rate in buffalo appears to be low, in contrast to that in cattle.

The African buffalo also has been shown to be susceptible to *T. mutans* infection.[27]

Brocklesby[7] described another new species, *T. barnetti,* from buffalo in Kenya in 1965. He found this parasite to differ from the other buffalo *Theileria* in two major respects: its macroschizonts were much larger than those of *T. parva, T. lawrencei* and *T. mutans,* and they contained a greater average number of nuclei than those of *T. parva.* Attempts to transmit *T. barnetti* between buffalo and from buffalo to cattle, using *R. appendiculatus* ticks, failed.

Theilerioses of Other Wild Mammals

Intraerythrocytic piroplasms of the genus *Theileria* have been reported from many species of wild mammals of the families Bovidae and Giraffidae in East Africa.[11,27] Schizont stages were also detected in four species: macroschizonts in the spleen of Coke's hartebeest (*Alcelaphus buselaphus cokii*),[11] eland (*Taurotragus oryx*),[4,22,27] and topi (*Damaliscus korrigum*),[27] schizonts in the kidneys of eland,[22] and macroschizonts and microschizonts in the spleen, lungs and lymph nodes of the reticulated giraffe (*Giraffa reticulata*).[11] All attempts to transmit these theilerial parasites to cattle have failed. The only *Theileria* of these wild mammals to have been named is *T. gorgonis*[10] of the blue wildebeest (*Connochaetes taurinus*).

The susceptibility of these wild animal species to *T. parva* and *T. lawrencei* infections is unknown. Attempts to infect eland with *T. parva* have been unsuccessful.[5,21]

Cytauxzoonoses of Wild Mammals

A new genus, *Cytauxzoon,*[31] was added to the protozoan family Theileriidae[15] by Neitz. This genus differed from *Theileria* in that schizogony occurred in the histiocytes rather than in the lymphocytes, but the intraerythrocytic piroplasms of both genera were morphologically indistinguishable. However, Levine[20] has recently published a new scheme of classification for the family Theileriidae, in which he suggests that *Cytauxzoon* should be considered a synonym of *Theileria.*

Cytauxzoon parasites have been recorded from four wild animal species only. They are *C. sylvicaprae*[31] from grey duiker (*Sylvicapra grimmia*), *C. strepsicerosi*[30] from greater kudu (*Tragelaphus strepsiceros*) and *Cytauxzoon* sp. from giraffe (*Giraffa camelopardalis*)[25] in South Africa, and *C. taurotragi*[5,24] from eland in Kenya. In all cases the parasites appeared to have been pathogenic. The theilerial schizonts found in a reticulated giraffe in Kenya[11] bore some resemblance to *Cytauxzoon* and have been listed as a doubtful record of this organism.[25]

The eland infected with *C. taurotragi* macroschizonts also showed a piroplasm parasitemia in excess of 90% before death.[24] Adult *R. appendiculatus* and *R. pulchellus* ticks, which fed as nymphs on this eland, were found to be infected with a *Theileria*-like parasite.[5] Attempts were made to transmit this parasite to another eland and to cattle. The only successful transmission was to a domestic cow through *R. pulchellus*: this animal underwent a febrile reaction with *Theileria*-like macroschizonts demonstrable in a parotid lymph node and piroplasms in erythrocytes.

Haematoxenus Species of Wild Mammals

A third genus, *Haematoxenus*, was added to the Theileriidae by Uilenberg.[37] He described the species *H. veliferus* from splenectomized cattle in Madagascar. This parasite was associated with erythrocytes and closely resembled theilerial piroplasms, except for the presence of a delicate lateral veil. Recently, *Haematoxenus* has been reported from African buffalo in the Central African Republic[38] and Uganda,[42] and from impala in Tanzania.[19] There was no evidence that *Haematoxenus* was pathogenic for either cattle or wild animals.

EXPERIMENTAL STUDIES

African Buffalo Theileria

Two buffalo (B1 and B2) were captured in the Serengeti National Park of Tanzania when less than 3 weeks of age,[40] and four were captured in the Laikipia District of Kenya: buffalo KB1, KB2 and KB4 from Solio Ranch, Naro Moru, when less than one year of age, and buffalo KB5 from Sirimma Farm, Ngobit, when 2 months old.[13,34] All buffalo were shown to be naturally infected with theilerial piroplasms, with peak parasitemias ranging from < 0.1 - 1.5%, and, in addition, KB5 was found to be harboring theilerial macroschizonts.

R. appendiculatus nymphs were applied to the ears of each buffalo. Batches of the resultant adult ticks were found to be infected with *Theileria* by examination of their salivary glands.[40] When similar batches of adult ticks from each buffalo were applied to the ears of individual steers, each batch transmitted fatal theilerial infections to cattle. These bovine reactions were typical of *T. lawrencei* infection.[40] By repeated application of nymphal ticks to captive buffalo, and subsequent testing of the infectivity of the resultant adults on cattle, it was demonstrated that buffalo can be continually infective for ticks over a period of at least 3 months.

T. lawrencei macroschizonts were isolated from buffalo KB5 and grown in a culture suspension of buffalo lymphoid cells.[34] Eight separate isolates were made from KB5 over a 5-month period. This technique provided a practical source of *T. lawrencei* antigen from buffalo for serological studies using the indirect fluorescent antibody (IFA) test. The sera of the five buffalo tested showed significant IFA titers to both buffalo-derived and cattle-derived *T. lawrencei*, and to *T. parva*, cell culture schizont antigens, using an anti-bovine conjugate.[13] However, the titers of individual serum samples to each antigen were indistinguishable, demonstrating the complete cross-identity of *T. lawrencei* and *T. parva* in the IFA test.

Wildebeest Theileria

Two blue wildebeest (SW1 and SW2) were captured when young in the Serengeti National Park, and two (W1 and W2) on the Athi/Kapiti Plains of Kenya. Splenectomy of the four wildebeest revealed that all were harboring *T. gorgonis*. W1 and W2 reacted fatally following splenectomy, with dramatic increases in theilerial parasitemias to 72% and 82% respectively, and evidence of hemoglobinuria and anemia before death.[32] W1 also developed *Anaplasma marginale* parasitemia, reaching a peak of 18%.[32,33]

Nymphal *R. appendiculatus* were applied to the ears of SW2 and W2 following splenectomy. The resultant adult ticks were found to have become infected with a theilerial parasite, but they failed to transmit theileriosis to steers.[32]

Blood was collected into heparin from the splenectomized wildebeest W1 and W2 and immediately 50 ml from each animal was inoculated intravenously into each of a pair of splenectomized calves. These attempts to transmit *T. gorgonis* by blood passage to cattle failed, but *A. marginale* was transmitted by this technique from W1 to the pair of recipient calves.[32,33]

A *T. gorgonis* piroplasm antigen was prepared from W2 and serological studies, using the IFA test, indicated that *T. gorgonis* was antigenically distinct from *T. parva, T. lawrencei* and *T. mutans*.[12]

Eland Theileria

Seven eland, held in semi-domestication in Kenya, were used. Four were held at the Mount Kenya Game Ranch, Nanyuki, and three at the Galana Game Farm Research Project east of the Tsavo National Park.[18] The eland were captured locally, except for three from the Mount Kenya Game Ranch which were captured at Maralal in the Samburu District of Kenya. Theilerial piroplasms were detected in small numbers ($< 1\%$) in the erythrocytes of all eland.

R. appendiculatus nymphs were applied to one ear, and *R. simus* nymphs to the other ear, of each eland. Of the resultant adult ticks, both species that engorged on Mount Kenya eland were found to be infected with theilerial parasites, but no evidence of tick infection was detected in either species from the Galana eland. Adult ticks from both ranches failed to transmit theileriosis to cattle.[18]

DISCUSSION

In many areas of East, Central and southern Africa, buffalo have been implicated in the epidemiology of theileriosis pathogenic for cattle.[3,8] Healthy African buffalo from Kenya and Tanzania were shown to harbor strains of *T. lawrencei* that were highly pathogenic for cattle. The four Kenyan buffalo were captured from cattle ranches in a *T. lawrencei* endemic area in which buffalo abound.[14] In contrast, the two Tanzanian buffalo were captured from herds in the Serengeti National Park which had had no contact with cattle. Thus, *T. lawrencei* (Serengeti) must be maintained by game animals, and the high prevalence of theilerial piroplasms in Serengeti buffalo (95% of 120 examined)[40] would suggest that this species is an important reservoir host of this parasite.

Buffalo were found to be continually infective for ticks over an extended period of time, and these ticks readily transmitted fatal *T. lawrencei* infections to cattle. All captive buffalo were shown to have persistent low-level theilerial parasitemias and, from buffalo KB5, *T. lawrencei* macroschizonts were regularly isolated in cell culture over a 5-month period. These results suggest that the *T. lawrencei* carrier status of buffalo may be associated with the continuous presence of schizonts from which piroplasms infective for ticks develop.

It is evident that the importance of *T. lawrencei* in pathogenic bovine theilerioses needs to be evaluated in all areas where this disease complex exists in association with African buffalo. Two recently developed techniques could provide relatively simple methods of determining the prevalence of *T. lawrencei* in wild buffalo populations. They are the isolation in cell culture of *T. lawrencei* macroschizonts from buffalo,[34] and the detection of *T. lawrencei* antibodies in buffalo sera using the IFA test.[13]

The unsuccessful attempts to transmit theilerial parasites from wildebeest and eland to cattle confirm previous studies[10,11] and suggest that such transmissions are unlikely to occur under normal field conditions. In these experiments much larger numbers of ticks were used than are likely to be involved in the field. Also, the possibility of transmission from wildebeest or eland to cattle is further precluded by the fact that ticks, shown to contain *Theileria*-like parasites in their salivary glands, were used in the experiments. Other reports have shown that rhipicephalid ticks can become infected with *Theileria*-like parasites following engorgement on wild antelope: *R. appendiculatus* from wildebeest[10] and eland,[5,24] *R. pulchellus* from eland,[5] and *R. evertsi* from impala (*Aepyceros melampus*).[19] Since only *R. appendiculatus* and *R. simus* were used in the above transmission experiments, further studies should be conducted using other tick species, and particularly *R. evertsi* and *R. pulchellus*, both of which have been shown to transmit *T. parva* to cattle.[6,27] Also, Brocklesby[5] managed to transmit a *Theileria*-like parasite from an eland infected with *C. taurotragi* to a cow through *R. pulchellus*.

There is considerable confusion over the identity of the intraerythrocytic piroplasms of wild mammals. The piroplasms of the genera *Theileria* and *Cytauxzoon* are morphologically indistinguishable, and Neitz[25] has suggested that many of those recorded as *Theileria* sp. may be eventually identified as *Cytauxzoon* sp. However, Levine,[20] in his recent reclassification of the piroplasms, has suggested that *Cytauxzoon* should be considered a synonym of *Theileria*. Some of this taxonomic confusion may be clarified by serological studies of these piroplasms. An example of this approach is the work on *T. gorgonis*.[12] A piroplasm antigen of this parasite was prepared from a splenectomized wildebeest and antisera to *T. gorgonis* was produced by inoculation of infected wildebeest blood into splenectomized calves. The *T. gorgonis* antigen was compared with standard antigens of *T. parva, T. lawrencei* and *T. mutans* in the IFA test, using bovine antisera to each parasite and an anti-bovine conjugate. The results indicated that *T. gorgonis* was antigenically distinct from the three bovine *Theileria* species, supporting Brocklesby and Vidler's[10] decision to give this theilerial parasite a specific name.

Barnett and Brocklesby[2,3] considered *T. lawrencei* to be a buffalo-modified strain of *T. parva* and, consequent to this, Levine[20] classified *T. lawrencei* as a synonym of *T. parva*. Barnett and Brocklesby based their contention on the immunity of *T. lawrencei*-recovered cattle to *T. parva* challenge and on the transformation of *T. lawrencei* on passage through cattle to a type behaviourally indistinguishable from *T. parva*. However, recent studies have shown that cattle immune to *T. parva* showed little resistance to challenge with non-transformed *T. lawrencei* (that is, *T. lawrencei* direct from buffalo), while cattle immune to *T. lawrencei* were fully resistant to *T. parva* challenge.[41] These differences in the cross-immunity between strains of *T. lawrencei* and *T. parva* in cattle demonstrate important immunological differences between the two parasites, and hence they cannot be considered synonyms for one another. Further studies to elucidate the relationships between *T. lawrencei* and *T. parva* should include work with susceptible buffalo.

The transmission of *Anaplasma marginale* from wildebeest to cattle by blood passage[32,33] was an interesting by-product of the *T. gorgonis* studies. Using similar techniques, Lohr and Meyer[23] transmitted *Anaplasma* species from wildebeest, Coke's hartebeest and Thomson's gazelle (*Gazella thomsonii*) to splenectomized calves. The wildebeest used in both studies were from the Kapiti Plains of Kenya. These results are of some importance, since anaplasmosis is another major disease of cattle in East Africa.

In conclusion, African buffalo are very important hosts of *T. lawrencei* in East Africa. Areas where African buffalo and the tick *R. appendiculatus* interact, must be considered potential *T. lawrencei* endemic areas. Introduction of cattle into such areas must be accompanied by an appreciation of the problems of Corridor disease. The role of other wild mammals in the epidemiology of bovine theilerioses remains unclear, but it is certain that they play a role in the maintenance of rhipicephalid tick populations.[30]

Acknowledgments

The experimental studies described in this paper were carried out by the FAO/UNDP Immunological Research on Tick-borne Cattle Diseases and Tick Control Project at EAVRO. I was a member of this project from 1968-1973, and gratefully acknowledge the permission of my colleagues to publish this review.

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Received for publication 11 August 1974