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Summary: Rinderpest was not recorded in cattle or wildlife in S. Kenya or Tanzania from 1965 to 1982. In W. Uganda the disease was not seen after 1944/45.

During the period 1967 to 1971, more than 1,525 sera from wildlife species in E. Africa, collected mainly by biologists and wildlife veterinarians, were examined for rinderpest-neutralising antibody.

Buffaloes showed no material evidence of infection in W. Uganda (1/77 positive) but the disease probably occurred in E. Kenya in 1969/70. In the Serengeti area of Tanzania one batch of sera collected in August 1969 showed low antibody titre ($10^{0.75}$ or less) in 7 of 15 animals 2 to 5 years old. This activity was restricted both geographically and temporally, as well as being difficult to assay in tube neutralisation tests.

No serological evidence of rinderpest in wildebeest was obtained after 1962.

In Uganda and Kenya no antibody was detected in warthogs. Low-titre neutralising activity was found in 5 of 58 Serengeti warthogs estimated to have been born in 1965/68.

Young eland from E. Kenya had high antibody titres in 1970. One suspicious animal was detected in S. Kenya; the evidence from Tanzania was inadequate.

Impala, Thomson’s gazelle, Grant’s gazelle, topi, Uganda kob, bushbuck and oryx were consistently negative.

High-titre antibody was commonly present in waterbuck (Kobus defassa) in W. Uganda and also in collections from the same species in the Rift Valley and Lake Provinces of Kenya. Another species (K. ellipsiprymnus) did not have any antibody in S. Kenya. The prolonged absence of rinderpest from the former areas, failure to spread to highly susceptible species and the presence of antibody in juveniles, suggested continuous infection with a rinderpest-related morbillivirus. Waterbuck sera were highly cytotoxic.

It was concluded that there was no adequate evidence for a persistent reservoir of rinderpest virus infection in E. African wildlife during the period 1967-71.

KEYWORDS: Africa - Rinderpest - Serological surveys - Viral disease - Wild animals.

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INTRODUCTION

Rinderpest virus infection used to be virtually an annual occurrence in wildebeest and buffaloes in the Serengeti and Mara areas of Tanzania and Kenya (Figs. 1 and 2). During the period 1960 to 1966 it was established, primarily by serological surveys, that most districts were free from infection after 1963 (13, 17, 31). A single focus of infection in cattle was demonstrated in the Loliondo area of Tanzania in 1965/66, with very infrequent spread to wildebeest. Thereafter, until 1971 no rinderpest was confirmed in domestic or wild animals, though every opportunity was taken to monitor wildlife populations, anywhere in East Africa, by testing sera made available from game-cropping, range-management or ecological programmes (for Kenya see 5, 6).

The results of these investigations have been summarised elsewhere (14), but it has become desirable to record them in greater detail, especially in view of later reports that seropositive animals occurred in some species, in buffaloes in Kenya in particular, during the 1970's (7, 8, 9) and early 1980's. More recently, severe disease has been recorded among buffalo, giraffe, warthog and eland in the Serengeti, and possibly the Tarangire National Parks of Tanzania, confirmed virologically as rinderpest (22, 23, 33).

The apparent disappearance of rinderpest from cattle and wildlife in the Serengeti-Mara region after 1965/66 was important in that it represented the culmination of decades of intense efforts to eradicate the disease by annual mass vaccination; it was also an important factor in the remarkable eruption of the wildebeest and buffalo populations which followed (26).

MATERIALS AND METHODS

Sera

Blood was usually collected from the severed vessels of animals which were shot, or from the jugular vein of those immobilised. Samples were chilled and serum decanted and/or clarified by centrifugation as soon as possible after collection; antibiotics or chloroform were often used as preservatives. Storage was at -20°C or below, and thawed aliquots were inactivated at 56°C for 30 m before testing.

Virus

Large batches of the attenuated Muguga strain of rinderpest virus at 90 or more passages in calf kidney cells were stored in glass-sealed ampoules at -20°C or lower. Several ampoules were pooled for each test and the contents diluted to give an estimated $10^{1.8}$ to $10^{2.8}$ TCD$_{50}$, checked by simultaneous titration in twofold dilution steps, using 5 tube cultures of primary calf kidney cells per dilution (18).

Virus neutralisation tests

Undiluted sera were first tested against a standard dose of virus, but when cytotoxicity was present or suspected, a 2-fold or 3-fold dilution was employed as an alternative or additional measure. Positive samples were assayed in 2-fold or, occasionally, 3-fold dilution series, following the tube culture techniques already described (14).
FIG. 1

The Serengeti National Park, Tanzania, with localities referred to in the text
Localities from which wildlife sera were collected in Kenya
(slightly modified after FAO, 1978)
RESULTS

Buffalo (*Syncerus caffer* Sparrman)

As this species is probably the most susceptible of all wild ungulates and usually suffers severely when infected, it will be considered first. The figures for sera from animals sampled in three East African countries, between 1967 and 1971, are given in Tables I to III.

**Table I**

Rinderpest-neutralising antibody in the sera of Uganda wildlife, Ruwenzori National Park, 1968-71

<table>
<thead>
<tr>
<th>Species*</th>
<th>No. positive/No. examined in age group</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>≤6M  7-12M  13-24M  25-36M  37-48M  5-6Y  7-8Y  ≥9Y</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Buffalo</td>
<td>0/1</td>
</tr>
<tr>
<td></td>
<td>Warthog</td>
<td>0/19</td>
</tr>
<tr>
<td></td>
<td>Topi</td>
<td>0/31</td>
</tr>
<tr>
<td></td>
<td>Uganda kob</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Reedbuck</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Waterbuck</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bushbuck</td>
<td></td>
</tr>
</tbody>
</table>

* For systematic Latin names, see text.
° Positive estimated to be 9 years old, titre $10^{0.69}$.
* All sera were cytotoxic. Titre of positives $\geq 10^{2.7}$.

**Table II**

Rinderpest-neutralising antibody in the sera of Kenya wildlife, 1967-71

<table>
<thead>
<tr>
<th>Species*</th>
<th>No. positive/No. examined in age group</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult</td>
<td>Subadult</td>
</tr>
<tr>
<td>Wildebeest</td>
<td>3/104°</td>
<td>0/15</td>
</tr>
<tr>
<td>Buffalo</td>
<td>3/11</td>
<td>-</td>
</tr>
<tr>
<td>Eland</td>
<td>0/22</td>
<td>1/18</td>
</tr>
<tr>
<td>Thomson’s gazelle</td>
<td>0/107</td>
<td>0/47</td>
</tr>
<tr>
<td>Grant’s gazelle</td>
<td>0/64</td>
<td>0/7</td>
</tr>
<tr>
<td>Impala</td>
<td>0/51</td>
<td>0/17</td>
</tr>
<tr>
<td>Coke’s hartebeest</td>
<td>0/93</td>
<td>0/16</td>
</tr>
<tr>
<td>Oryx</td>
<td>0/6</td>
<td>0/1</td>
</tr>
<tr>
<td>Giraffe</td>
<td>0/9</td>
<td>0/29</td>
</tr>
<tr>
<td>Warthog</td>
<td>0/8</td>
<td>0/7</td>
</tr>
</tbody>
</table>

* For systematic Latin names, see text.
° For details of positives, see text.
### TABLE III

*Rinderpest-neutralising antibody in the sera of N. Tanzanian wildlife, 1967-71*

<table>
<thead>
<tr>
<th>Species*</th>
<th>No. positive/No. tested in age group (year of birth)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buffalo</td>
<td>0/7</td>
<td>0/3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wildebeest</td>
<td>1/14</td>
<td>0/4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eland</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Thomson's gazelle</td>
<td>0/1</td>
<td>0/1</td>
</tr>
<tr>
<td>Grant's gazelle</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Impala</td>
<td>-</td>
<td>0/1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topi</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Coke's hartebeest</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Warthog</td>
<td>0/5</td>
<td>1/13</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*For systematic Latin names, see text.*
In the Ruwenzori (previously Queen Elizabeth) National Park (RNP), Uganda, neutralising antibody was detected in only one of 77 animals (Table I). This was estimated to be 9 years old in 1968, its $\log_{10} \text{VN}_{50}$ titre being $10^{0.69}$. As the last recorded outbreak of rinderpest in this area was in 1944/45 (18), there was no ready explanation for the result; the only other species with rinderpest-neutralising antibody was the *Defassa* waterbuck, as will be discussed later.

Very few adequately identified sera became available from Kenyan buffaloes during the years 1969/70; three of 11 adults were positive, all being derived from the south (Mara and Kiboko; see Fig. 2), but no precise age estimate was available and they could well have been infected prior to 1964/65. A yearling which was seropositive in 1970 was from a ranch in the east (Galana), where seropositive eland were also present simultaneously (see below); they could easily have become contaminated from other infected wildlife moving from the north. The other two positive buffaloes were calves about six months old and their antibody was probably passively acquired.

Details for buffaloes from the Serengeti area of Tanzania are given in Table IV, the summary being in Table III. Of 35 sera derived from animals born during or before 1962 and taken in 1967/69, 27 or 77% were positive, the titres ranging widely from $10^{0.35}$ to $10^{2.55}$ (mean $10^{1.61} \pm 10^{0.70}$). As was to be anticipated from the transfer of maternal antibody, 6 calves between 6 to 9 months old were all seropositive in 1967, with titres varying from $10^{0.25}$ to $10^{1.55}$. Surprisingly, however, 10 born in 1968/69 were all negative at the time of sampling.

### Table IV

**Rinderpest-neutralising antibody in Tanzanian buffaloes, Serengeti National Park, 1967-69**

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct/67</td>
<td>Mbalageti River</td>
<td>-</td>
<td>-</td>
<td>6/6$^a$</td>
<td>0/3</td>
<td>0/3</td>
<td>0/1</td>
<td>2/3</td>
<td>17/21</td>
</tr>
<tr>
<td>Mar/Jul/68</td>
<td>Kilimafеza, Simba,</td>
<td>-</td>
<td>0/1</td>
<td>0/2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5/6</td>
<td></td>
</tr>
<tr>
<td>Mar/69</td>
<td>Musabi</td>
<td>-</td>
<td>-</td>
<td>0/2</td>
<td>0/1</td>
<td>0/3</td>
<td>-</td>
<td>-</td>
<td>3/3</td>
</tr>
<tr>
<td>Aug/69</td>
<td>Mbalageti River</td>
<td>0/2</td>
<td>1/4$^*$</td>
<td>2/5$^*$</td>
<td>2/3$^*$</td>
<td>2/3$^*$</td>
<td>-</td>
<td>3/4$^*$</td>
<td></td>
</tr>
<tr>
<td>Dec/69</td>
<td>Kogatendi (Wogakuria)</td>
<td>0/5</td>
<td>0/2</td>
<td>0/2</td>
<td>-</td>
<td>-</td>
<td>0/2</td>
<td>-</td>
<td>1/1</td>
</tr>
</tbody>
</table>

$^a$ Probably passive antibody, titre $10^{0.25}$ to $10^{1.55}$, in animals up to 9 months old.

* Titres very low, $10^{0.39}$ to $10^{0.75}$.

* Titres $10^{1.69}$ to $10^{2.47}$.

Anomalous results were recorded for a collection from animals near the Mbalageti river in August 1969 (Table IV and Fig. 1); antibody of low titre ($10^{0.39}$ to $10^{0.75}$) was found in 7 of 15 animals estimated to be between the ages of 2 to 5 years only. The mean titre for the seven animals was found to be $10^{0.51} \pm 10^{0.13}$, a figure which was not, however, significantly different from that for all buffaloes probably infected prior to 1963 ($t = 1.601; 0.1 < p < 0.2$) but obviously lower than those for three animals.
more than 8 years old collected simultaneously in the same locality ($10^{1.69}$ to $10^{2.47}$). It was found in repeated screening tests, using undiluted sera against a standard dose of virus, that sometimes the weakly “positive” samples appeared to be completely non-protective or, more commonly, they protected only a fraction of the cultures. Such sera were always titrated and if they again exhibited any neutralising activity, they were classed as positive (Table IV). Delays in obtaining further samples for retesting may have been important in some instances. Antibody was absent from few animals of the 2 to 5 years age group sampled in 1969 in two other localities of the Serengeti Park (Musabi and Wogakuria; Table IV, Fig. 1).

Wildebeest (*Connochaetes taurinus* Burchell)

This species, which was commonly infected and often suffered from rinderpest morbidity and mortality in the years to 1963 (17), is absent from W. Uganda and was therefore investigated only in S. Kenya and N. Tanzania. Table II shows that, of 119 animals from which serum was obtained in Kenya between July 1967 and March 1971, only 3 were positive. The areas from which animals were derived included Kajiado, Amboseli, Narok, Mara and Loita districts (Fig. 2), in all of which a variable proportion of wildebeest, probably about 20-80% (13, 17, 31) were positive prior to 1964. The three positives detected here were all classed as adults, two of them being considered “old”; only serum from a single adult was titrated and found to have a very low endpoint, namely, $10^{0.35}$. Hence these animals were probably infected when rinderpest was still enzootic in the region.

In Tanzania a total of 177 wildebeest sera was collected between May 1967 and January 1971. Most of these were from the Kirawira and Seronera localities (Fig. 1) or adjacent to it in the Serengeti National Park, i.e. they included both migrant and resident populations (31); some 79 of them were derived from animals for which no ages were provided and 27 of these came from the Loliondo district, outside the Park, in 1968. All of the 58 animals born in the years 1967 to 1969 inclusive (Table III) were less than one year old; the 3 positives were presumably calves with passive antibody (titres $10^{0.39}$ and $10^{0.63}$ in 2 cases). The other 5 seropositive animals of known age had been born during or before 1963 and in the two cases which were assayed had very low titres ($10^{0.39}$). Of 27 sera from unclassified “adult” animals shot at Loliondo in 1968, 9 (33%) were positive, probably as the result of infection prior to 1966 (31). Six of these samples were titrated, the mean titre being $10^{0.53} \pm 0.15$ with a range of $10^{0.33}$ to $10^{0.73}$. This was somewhat lower than the average recorded in similar animals up to 1965 when the mean titre in seven 4-year-old animals was $0.83 \pm 0.54$ (31).

Warthog (*Phacochoerus aethiopicus* Pallas)

Serum was obtained from 104 warthogs in the Ruwenzori National Park, 99 of them between January and December 1968. Table I shows that these were all seronegative, irrespective of age group. In Kenya a much smaller number (15) from southern localities (Nguruman, Kajiado, Loita) were consistently negative (Table II, Fig. 2).

Sera were also obtained from 73 Tanzanian warthogs, of which 72 were shot in the Kirawira area, immediately north of the Serengeti National Park, during the period November 1967 to October 1970, but mainly (52 of 72) during 1969 (Table III, Fig. 2). Occasional animals (5 of 58) born in the years 1965 to 1968 exhibited rinderpest-
neutralising activity although they had not been exposed to any known outbreaks of rinderpest. Titres were consistently low or very low, varying from an unquantifiable trace to $10^{0.99}$. In one case at least, a 2-month-old animal, the antibody was probably maternal in origin. In addition, 3 of 10 animals estimated to be 4 years or more of age in 1969 also had low titre antibody — ranging from a trace to $10^{0.75}$ — and in these cases it was not possible to exclude infection prior to the disappearance of overt rinderpest.

**Impala (Aepyceros malampus Lichtenstein)**

Sixty-eight serum samples were obtained from impala in Kenya, most of them (> 40) being collected during 1970/71 in the old southern enzootic areas for rinderpest (Sultan Hamud, Kiboko, Kajiado, Ngong, Akira, Loita). As shown in Table II, none of them had rinderpest-neutralising antibody.

In Tanzania sera were collected sporadically from April 1967 to January 1971; 106 of them were provided in the course of a species biology project conducted in the Serengeti National Park (SNP) and accompanied by accurate ageing of animals killed. The overall results are given in Table II and those for the SNP project in Table V.

**TABLE V**

**Rinderpest-neutralising antibody in the sera of impala from the Serengeti National Park, Tanzania, March 1969 to December 1970**

<table>
<thead>
<tr>
<th>No. positive/No. tested in age group</th>
<th>6-11M</th>
<th>12-18M</th>
<th>1.5-2Y</th>
<th>2.5-3Y</th>
<th>3-4Y</th>
<th>4-6Y</th>
<th>5-7Y</th>
<th>7-9Y</th>
<th>&gt;10Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0/8</td>
<td>0/6</td>
<td>0/11</td>
<td>0/8</td>
<td>1/23*</td>
<td>0/30</td>
<td>0/3</td>
<td>0/7</td>
<td>2/10*</td>
<td>3/106</td>
</tr>
</tbody>
</table>

* One assayed; titre $10^{0.45}$.

It was apparent that antibody was very infrequent and of very low titre; the positive sera in those 10 years old or more were probably attributable to infection prior to 1963.

**Eland (Taurotragus oryx Pallas)**

As one of the species most susceptible to rinderpest, the eland has often been prominent in outbreaks of the disease but it was very difficult to obtain enough serum samples for epidemiological investigations.

In Kenya samples were obtained from 34 animals over the period January 1968 to August 1970 (Table II). These were derived from the old southern enzootic area (Kajiado, Sultan Hamud, Kiboko, Akira) with the exception of 5, including 4 juveniles, from the Galana Ranch in the northeast of the country, in August 1970 (Fig. 2). Two of the latter had high titre antibody ($10^{2.28}$ and $10^{2.76}$ respectively), almost certainly the result of natural infection. The other positive animal was a subadult from Sultan Hamud in 1969 and the titre of $10^{0.93}$ was conspicuously lower; there was no explanation for its occurrence.
From Tanzania, only 8 sera were obtained and the single positive was estimated to have been born in 1963. Allowing for difficulties in ageing, it could have been infected towards the end of the enzootic; its titre was $10^{1.0}$.

**Thomson’s gazelle (Gazella thomsonii Günther) and Grant’s gazelle (Gazella grantii Brooks)**

Only the first of these two species was considered to have been infected in the period of enzootic rinderpest in N. Tanzania and S. Kenya, but not more than 10% were serologically positive in 1962/63 in the Ngorongoro Crater where rinderpest infection occurred frequently until 1962 (17, 31). From April 1967 to January 1971, 121 sera were obtained from Thomson’s gazelle in the Serengeti and Loliondo areas and two possible positives were encountered. In one case, undiluted serum from an animal born in 1965, protected only 2 of 5 cultures; in the other, from a gazelle which was not aged, the titre was very low ($10^{0.33}$).

In Kenya, 163 sera from Thomson’s gazelle collected mainly in the south from mid-1969 to early 1971, but some also from the Rift Valley (Suguroi), were uniformly negative, as were also 71 sera from Grant’s gazelle derived exclusively from the south (Table II).

**Waterbuck (Kobus ellipsiprymnus Ogilby and K. defassa Rupell)**

These two species overlap in their ranges in Kenya, and according to Stewart and Stewart (29), it may be difficult to differentiate them in these localities. Hence the identifications used here are those provided by the collectors, but could be difficult to substantiate.

An additional difficulty encountered with waterbuck serum, especially from *K. defassa*, was that it tended to be highly cytotoxic at low dilutions to the cell cultures (primary bovine kidney, testis or thyroid cells) commonly used in tests for virus-neutralising antibodies (see, for example, 21). It was therefore impossible to screen many of the samples from these species in undiluted form and, in titrations, some cytotoxicity was frequently seen at dilutions of 1:4 or even 1:16. Other tests of equal sensitivity and specificity were not readily available at the time.

Six *K. defassa* sera collected in the RNP Uganda in 1970 (Table I) were successfully screened and at least 2 of these from animals only 12-18 months old were positive, with VN$_{50}$ titres at least $10^{2.7}$ against a high dose of virus ($10^{2.55}$). In Kenya samples were collected from 17 *K. defassa*, 16 being from a single ranch in the Rift Valley Province (Nderit Estate, Nakuru — later incorporated into the Lake Nakuru National Park). Fifteen of them were obtained during September and October 1970. Ten further sera from the “common” or “ringed” waterbuck (*K. ellipsiprymnus*) were collected from the old southern enzootic area in 1969/70 (Kiboko, Makindu). Table VI gives the results of examination of these sera.

It was evident that *K. defassa* usually possessed rinderpest-neutralising antibody to high or very high titre; one animal from the Lake Province (Lambwe Valley) was also positive. Hence, the geographical distribution of this activity in waterbuck may have been extensive in Kenya as well as occurring in W. Uganda; the widespread occurrence of antibody in *K. defassa* classed as “juvenile” was also worthy of note. In contrast, no antibody was detected in 5 sera from *K. ellipsiprymnus* in S. Kenya.
TABLE VI

Rinderpest-neutralising antibody in Kenyan waterbuck sera

<table>
<thead>
<tr>
<th>Species</th>
<th>No. positive/No. successfully tested*</th>
<th>Titres of positives</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult</td>
<td>Subadult</td>
</tr>
<tr>
<td><em>K. defassa</em></td>
<td>3/3</td>
<td>3/3</td>
</tr>
<tr>
<td></td>
<td>(6)</td>
<td>(5)</td>
</tr>
<tr>
<td><em>K. ellipsiprymnus</em></td>
<td>0/4</td>
<td>0/1</td>
</tr>
<tr>
<td></td>
<td>(7)</td>
<td>(3)</td>
</tr>
</tbody>
</table>

* Figures in brackets refer to the totals available and tested. Failures were due to cytotoxicity.

Bohor reedbuck (*Redunca redunca* Pallas)

In Uganda (Table I) 11 Bohor reedbuck and from Kenya 4 of the same species were all negative, but a problem with cytotoxicity, similar to that encountered with waterbuck, sometimes necessitated screening sera at 1:2 or 1:3 dilution.

Giraffe (*Giraffa camelopardalis* Linnaeus)

Only in Kenya were appreciable numbers of sera obtained from giraffe, all of them being collected between mid-1969 and early 1971; one animal was reported to be of the rarer variety, *Giraffa reticulata* (De Winton). Many were obtained on a large ranch in the southern area (Akira, Fig. 2), others from the Rumuruti and Thika districts. No antibody was detected. However, a single specimen from an animal of unknown age in the Serengeti Park was positive in 1969 (titre $10^{0.57}$).

Coke’s hartebeest (*Alcelaphus cokii* Günter)

This species, which is generally regarded in E. Africa as highly resistant to rinderpest infection, was frequently sampled in Kenya between mid-1967 and March 1971, all animals being from districts in the old enzootic area (Kiboko, Amboseli, Kajiado, Loita Plains) and the Akira ranch. None of 110 serum samples was positive.

In Tanzania, a single doubtful positive was found in 11 samples from the SNP taken in January 1971; the “positive” appeared to be somewhat cytotoxic and was not titrated.

Other species

The RNP provided 14 samples from Uganda kob (*Adenota kob* Thomasi) and 39 topi (*Damaliscus korrigum* Ogilby) of varying age groups; only one of the latter was obtained from Kenya and 13 non-aged specimens from Tanzania (SNP, Table III). Uganda supplied 6 sera from bushbuck (*Tragelaphus scriptus* Pallas) in the RNP and Kenya 2 only (from the Lambwe Valley); none of these was cytotoxic. Kenya provided 7 sera from fringed-eared oryx (*Oryx beisa callotis* Thomas) of diverse origin. All of these specimens were negative. Finally, small numbers of sera from elephant (*Loxodonta africana* Schreber) and zebra (*Equus burchelli* Gray) were occasionally examined, together with a very few hyena (*Crocuta* sp.), rhinoceros (*Diceros*
bicornis), dik-dik (Rhinotragus sp.) and bushpig (Potamochoerus sp.). Although no positives were encountered, no conclusions could be drawn from such restricted samples.

DISCUSSION

Many of the results presented here have defects which are usually and almost inevitably associated with studies of microbiological infections in free-living mammals. These include:

- Inadequate sampling of the populations involved, whether in respect to overall numbers, adequate representation of different age-groups, spatial distribution within the study area and sequential collections in single localities. Fortunately these details were seldom of crucial significance in interpretation here, though it was unfortunate that the numbers of usable buffalo sera from the Serengeti region were so limited, in view of the importance of this species in the epidemiology of rinderpest or, for that matter, of other diseases such as pseudo-lumpy-skin disease, i.e. bovine herpesvirus 2 infection (24, 16).

- The single serological test employed (virus-neutralisation) was insufficiently sensitive to give clear-cut, repeatable results when the titres were very low and possibly not specific, as in some Serengeti buffaloes and warthogs. Group-specific tests for morbilliviruses, such as indirect immunofluorescence, immunoperoxidase or ELISA (1) would probably have been helpful, as would more opportunities for virus isolation.

Low titre (1:4 to 1:8) rinderpest-neutralising antibodies, presumably non-specific, have been recorded in a proportion of British or Caribbean cattle by Taylor and Rowe (30) using a microtitre test, but they did not occur in conventional tube tests such as were employed here. They have also been reported from cattle in New Caledonia – a Pacific territory never infected by the virus (Lefèvre, P-C., personal communication).

The high titre neutralising activity demonstrated in K. defassa in W. Uganda and in two widely separated areas of Kenya, all free for decades of disease showing any resemblance to rinderpest, poses a question as to its nature and origin. The cytotoxicity of waterbuck and, to a lesser extent, of reedbuck sera was a problem which we were not able to overcome completely by a single cycle of salt (ammonium sulphate) precipitation, in contrast to the later report by Rossiter et al. (22). Nevertheless, when the sera were titrated, higher dilutions often inhibited the virus without being cytotoxic, and clear endpoints were recorded (Table VI). Such cytotoxicity has been observed by others (20) in the same and other tube culture systems, e.g. in primary and secondary bovine thyroid cells; it was not reported (10, 11, 12) when secondary testis or kidney cells were used in microtitre plates.

Apart from the cytotoxicity, an extraordinary feature of the antiviral activity in waterbuck and reedbuck sera was the very high titres recorded. In addition to those for rinderpest, which were at least as high as those in very susceptible species infected by virulent strains, mean titres against bovine herpesvirus 1 (IBRV) were recorded as $10^{4.08}$ and $10^{3.32}$ (20) or 1:170 and 1:309 (10) for these species respectively, i.e. about 10 to 1,000 times higher than in any other seropositive wild animal. We found that 6 of 16 K. defassa and 8 of 9 K. ellipsiprymnus possessed neutralising antibody
to bovine diarrhoea pestivirus (BDV) and the mean titre for 7 of the latter was $10^{4.07 \pm 0.45}$, again about 100 times higher than in other positive species. Similarly, although Reid et al. (21) observed neutralising activity for alcelaphine herpesvirus 1 (malignant catarrhal fever virus) in waterbuck but considered it was possibly spurious, Hamblin and Hedger (11) found all 7 K. defassa and 11 K. ellipsiprymnus positive, as well as 5 of 7 reedbuck. Again the titres were higher in these 3 species than in any other, viz. in the range 1/45-1/1024. The reason for this wide-ranging and potent activity needs further investigation.

Assuming that the rinderpest-neutralising activity in K. defassa sera was virus-induced, then the infectious agent was probably widespread and continuously active in scattered and relatively small populations of this species. Waterbuck show a considerable affinity for riverine or lacustrine habitats often, as in the Ruwenzori National Park, heavily frequented by other rinderpest-susceptible species such as buffalo and warthog. As rinderpest did not occur in these indicator hosts, it is difficult to believe that the virus involved was, in fact, that of rinderpest. It could have been another morbillivirus which cross-reacts with rinderpest virus, like the bovine isolates from Germany (2) or the USA (3) or the hedgehog virus isolated in Britain (32). Furthermore, it is possible that this putative agent may be transferred occasionally to other species, such as buffalo and warthog, giving rise to the very low-titre rinderpest-neutralising antibody which was occasionally encountered after 1967. In this respect it is unfortunate that no waterbuck sera were available from the Serengeti National Park, particularly for the year 1969.

Scott (25) reviewed older reports on the susceptibility of wild species to rinderpest; in addition, there is good recent evidence that reedbuck are naturally very susceptible to some virulent strains of virus. An outbreak involving mainly reedbuck has been reported in E. Sudan (4). Waterbuck were reported to be "slightly affected" by a virulent wave of the disease in Kenya in 1960/62 (28) and more recently Kobus sp. died from presumed rinderpest in the Yankari Reserve during the epizootic in Nigeria (26). It is not known whether waterbuck develop disease associated with the proposed morbillivirus infection; deaths in K. defassa and impala to the east of the Nakuru National Park were reported in May 1968 and subsequently but were not investigated (Stewart, D.R.M., personal communication). The isolation of an agent and experimental infection, including inoculation of cattle, should rapidly provide this important information.

The serological evidence presented here does not support a case for long-term enzootic infection by rinderpest virus of small, isolated populations of wild ungulates such as has been postulated (22, 33). There is, however, an evident need to monitor wildlife populations serologically on an adequate and continuous basis, preferably with attempts to isolate and characterise the viruses involved. Rinderpest-related agents could well be active in some species, without necessarily presenting a greater risk to cattle than the "new" morbilliviruses already isolated in Europe and N. America (2, 3, 32).

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Au cours de la période 1967-1971, plus de 1 525 sérums provenant d’ animaux de différentes espèces sauvages d’Afrique de l’Est, recueillis pour la plupart par des biologistes ou des vétérinaires spécialistes de la faune sauvage, ont fait l’objet d’examens pour la recherche d’anticorps neutralisant le virus bovispestique.

Chez les buffles, aucune preuve sérologique d’infection n’a été constatée dans l’ouest de l’Ouganda (un sérum positif sur 77), mais la maladie a probablement sévi dans l’Est du Kenya en 1969-1970. Dans un lot de sérums recueillis en août 1969 dans la zone du Parc de Serengeti, en Tanzanie, des anticorps de titre peu élevé (10$^{0.75}$ ou moins) ont été décelés chez 7 animaux sur 15 âgés de deux à cinq ans. Il faut souligner les limites de cette enquête, dans l’espace et dans le temps, ainsi que les difficultés rencontrées pour le titrage par l’épreuve de neutralisation en tube.

Chez les gnous, aucune preuve sérologique de la présence de la peste bovine n’a été obtenue depuis 1962.

Chez les phacochères, il n’a pas été décelé d’anticorps en Ouganda ni au Kenya. Une activité neutralisante de titre peu élevé a été constaté chez 5 phacochères du Parc de Serengeti sur 58, nés selon les estimations entre 1965 et 1968.


Les impalas, les gazelles de Thomson et de Grant, les topis, les cobes de l’Ouganda, les guibs harnachés et les oryx ont régulièrement présenté des résultats négatifs.

Ces enquêtes ont abouti à la conclusion qu'il n'y avait aucune preuve convaincante de l'existence d'un réservoir persistant d'infection par le virus bovispestique dans la faune sauvage d'Afrique de l'Est pendant la période 1967-1971.


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Resumen: En el sur de Kenia y de Tanzania, la peste bovina no fue señalada ni en bovinos ni en animales salvajes entre 1965 y 1982. En el oeste de Uganda la enfermedad no se observa desde 1944-1945.

Durante el período 1967-1971, más de 1 525 sueros procedentes de animales de distintas especies salvajes de Africa del Este, recogidos en su mayoría por biólogos y veterinarios especialistas en esa fauna, fueron objeto de exámenes para la investigación sobre anticuerpos capaces de neutralizar el virus.

En el caso de los búfalos, ninguna prueba serológica de infección fue señalada en el oeste de Uganda (un seropositivo sobre 77) pero la enfermedad probablemente afectó el este de Kenia en 1969-1970. En un lote de sueros recogidos en agosto de 1969 en la zona del Parque de Serengeti, en Tanzania, anticuerpos de título poco elevado (10^{0.75} o menos) fueron descubiertos en siete animales sobre quince de una edad de dos a cinco años. Conviene subrayar los límites de esta investigación, tanto en el espacio como en el tiempo, así como las dificultades halladas para el titulado mediante la prueba de neutralización en tubo.

En los ñus, ninguna prueba serológica de presencia de peste bovina fue obtenida desde 1962.

En los facoqueros, no se descubrieron anticuerpos en Uganda ni en Kenia. Una actividad neutralizante de título poco elevado se señaló en cinco facoqueros del Parque de Serengeti sobre una cantidad de 58, nacidos según estimaciones entre 1965 y 1968.


Los impalas, las gacelas de Thomson y de Grant, los topis, los kobos de Uganda, los bushbuck (Tragelaphus scriptus) y los oryx presentaron regularmente resultados negativos.

Anticuerpos de título elevado se descubrieron a menudo en los kobos de-fassa (K. defassa) del este de Uganda, así como entre grupos de animales de la misma especie en las provincias del Valle del Rifi y del Lago, en Kenia. Otra especie (K. elliptiprymnus) carecía de anticuerpos en el sur de Kenia. El que estas regiones no hubieran sido alcanzadas por la peste bovina desde hacía mucho tiempo, la ausencia de propagación a las especies altamente sensibles y la presencia de anticuerpos en animales jóvenes hicieron pensar en una infección continua por un virus morbilli emparentado con el virus de la peste bovina. Los sueros de los kobos de-fassa presentaban fuerte citotoxicidad.
Estas investigaciones arrojaron como conclusión que no había ninguna prueba concluyente de la existencia de una reserva persistente de infección por el virus de la peste bovina en la fauna salvaje de África del Este durante 1967-1971.

PALABRAS CLAVE: África - Animales salvajes - Enfermedades virales - Investigaciones serológicas - Peste bovina.

**REFERENCES**


