FOOT-AND-MOUTH DISEASE AND THE AFRICAN BUFFALO *(SYNCERUS CAFFER)*.
1. CARRIERS AS A SOURCE OF INFECTION FOR CATTLE

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ABSTRACT

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Ten pregnant buffalo cows, six of which were subsequently shown to be carriers of SAT 1, 2 and 3 viruses, were captured in the Kruger National Park (KNP) and allowed to calve in captivity. The buffalo cows and calves were seperated by a fence from 6 FMD susceptible cattle but the buffalo and cattle were obliged to use common drinking troughs and hay racks. Over a period of 15 months, during which the buffalo calves lost their maternally-derived immunity, neither the buffalo calves nor the susceptible cattle became infected with FMD virus. By the end of the observation period, however, only 1 buffalo cow still had detectable virus in its oesophageal/pharyngeal specimens.

INTRODUCTION

The association of foot-and-mouth disease (FMD) with wildlife in southern Africa has been apparent for many years (Rossiter & Albertyn, 1947; Howell & Mansvelt, 1972). In particular the buffalo *(Syncerus caffer)* has been shown to be a maintenance host for the SAT types of FMD virus (Hedger, 1976a); the only free-living species for which this has been conclusively demonstrated.

Within buffalo populations evidence indicates that the virus is transmitted horizontally and most young buffalo acquire infection soon after maternally-derived passive immunity wanes sufficiently, i.e., between 3 and 8 months of age (Condy & Hedger, 1978). The majority of these infections are, however, inapparent (Hedger, 1976a).

Following infection the virus may persist in the pharynx of buffalo [these animals have been termed carriers (Hedger, 1976a)] for periods of up to at least 5 years (Hedger, 1976b; Anderson, Doughty, Anderson & Paling, 1979) and from the observation that SAT 1 and 2 could be maintained in a small isolated herd of buffalo (less than 100 animals) for at least 24 years (Condy, Hedger, Hamblin & Barnett, 1985), it must be concluded that carriers play a role in maintaining FMD virus in buffalo populations.

Despite the apparent ease with which the SAT types of FMD virus are transmitted between carrier and susceptible buffalo, attempts at showing that the same is possible between carrier buffalo and susceptible cattle have generally been unsuccessful (Condy & Hedger, 1974; Anderson *et al.*, 1979; Anderson, 1986). Recently, however, Hedger & Condy (1985) have reported transmission of SAT 3 from carrier buffalo to cattle after 2 years of close contact between the 2 species. Despite these contradictory findings, a strong belief, based on circumstantial evidence, exists among veterinarians in southern Africa that buffalo are generally the ultimate source of SAT viruses in FMD epidemics of domestic stock. This has led to control measures, including the eradication of buffalo from large farming areas in Zimbabwe (Seery, 1984) and game fencing aimed at minimizing contact between buffalo and cattle. Thus this problem has important implications for both the access of southern African countries to international meat markets and wild-life conservation and utilisation.

This and the following paper describe attempts to establish more clearly the threat posed by buffalo infected with SAT virus types to cattle and other species of wild-life. The investigation detailed here was designed to test the hypothesis that buffalo calves undergoing primary infection, are more likely than carrier buffalo to excrete quantities of virus sufficient to infect cattle in close proximity, especially if feeding and watering facilities are shared. The intention was to allow carrier buffalo cows to calve and raise their offspring in close proximity to susceptible cattle. It was predicted that the cows would infect their calves when the passively-acquired immunity of the latter declined to non-protective levels, i.e. after 3–8 months (Condy & Hedger, 1974; Condy & Hedger, 1978). It was further presumed that if the calves undergoing primary infection excreted large quantities of virus the susceptible cattle in an adjacent pen, sharing feed and water with the buffalo, would rapidly contract the infection.

MATERIAL AND METHODS

Animals

Ten adult buffalo cows, subsequently shown to be pregnant, were captured in the Lower Sabi/Crocodile Bridge area of the Kruger National Park (KNP) using a mixture of 10 mg etorphine hydrochloride[1] and 50 mg xylazine[2] inject by means of a projectile syringe. After pregnancy was confirmed by rectal examination in the field, 150 mg azaperone[3] was injected into each animal which was then transported in sternal recumbency to the experimental pens at Skukuza. On arrival at Skukuza the buffalo were sprayed with an acaricidal dip[4], dewormed[5], dehorned, branded and given an antibiotic cover[6]. At the same time blood samples for serum preparation and oesophageal/pharyngeal (OP) specimens (Hedger, 1968) were collected. Narcosis was reversed using diprenorphine hydrochloride. The buffalo were then released into pens B and C (Fig. 1) between which, for cleaning purposes, they were alternated for the next 15 months.

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TABLE 1 Carrier and antibody status of buffalo cows at the start and end of the observation period

Cow number	Calving date (calf No.)	November, 1981				November, 1982				February, 1983
		Carrier[1] status	Serum antibody titre[2]			Carrier[1] status	Serum antibody titre[2]			Carrier[1] status
			SAT 1	SAT 2	SAT 3		SAT 1	SAT 2	SAT 3	
1	03/02/82 (3)	NVI	2,1	2,3	2,3	NVI	2,0	2,6	2,0	NVI
3	aborted	SAT 3	2,1	2,0	2,9	SAT 3	2,1	2,6	2,7	NVI
4	12/02/82 (2)	NVI	2,9	2,6	2,7	NVI	2,7	2,6	2,4	NVI
5	13/03/82 (8)	SAT 1	2,7	2,1	2,3	NVI	2,7	2,3	2,4	NVI
6	04/02/82 (1)	NVI	2,0	2,4	2,1	NVI	1,8	2,4	1,5	NVI
7	17/03/82 (5)*	SAT 1	2,3	2,1	2,0	Dead (16/08/82)	—	—	—	—
8	19/02/82 (4)	SAT 3	2,0	1,8	2,4	SAT 3	2,0	2,0	2,4	SAT 3
12	25/12/81 (6)	NVI	2,4	2,0	1,3	NVI	2,1	1,7	2,0	NVI
13	22/03/82 (7)**	SAT 1	ND	ND	ND	NVI	2,0	1,7	2,3	NVI
15	25/02/82 (9)**	SAT 2	ND	ND	ND	NVI	1,8	2,6	2,0	NVI

[1] Virus isolated from OP specimen

[2] Log_{10} of the reciprocal of the 50% serum end-point dilution

NVI—No virus isolated
ND—Not done
*—Died aged 4 months
**—Died aged 2 weeks

Nine of the buffalo cows calved over the following 3 months and 1 aborted (No. 3, Table 1). Only 6 of the 9 calves survived more than 4 months, the other succumbing to coccidiosis. Treatment of the remaining animals with amprolium[1] prevented further mortality.

Six adult cattle, which had not previously been vaccinated against or infected with FMD virus, were kept continuously in pens adjacent to the buffalo (i.e. A or D, Fig. 1, depending on whether the buffalo were in pens B or C) for the following 15 months.

The partitions between individual pens consisted of iron railings approximately 30 cm apart and the entire perimeter of the pens was lined with closely packed dry reeds to a height of 2,5 m which was intended to prevent distrubance of the buffalo by movement of people and vehicles outside the pens. Communal hay-racks and water containers were provided for the cattle and buffalo (Fig. 1). Feed consisted of a mixture of lucerne (alfalfa) and teff (*Eragrostis* spp.) hay.

Disease monitoring and specimen collection

Serum and OP specimens were collected from the buffalo cows on 3 occasions over the 15 month observation period as shown in Table 1.

The buffalo calves were immobilized at fortnightly intervals using the same drug mixture as for adults (at appropriately reduced dosage rates) to allow examination for FMD lesions and collection of blood for serum preparation.

The cattle were examined weekly for evidence of FMD infection and bled at the same time. Care was taken to ensure that mechanical transfer of FMD virus from buffalo to cattle did not occur as a result of animal examination or specimen collection.

Laboratory procedures

Isolation of virus was made on monolayers of primary bovine thyroid cells in roller tubes and micro serum neu-

tralization (SN) tests for antibody carried out as described by Golding, Hedger, Talbot & Watson (1976) at the World Reference Laboratory for FMD[1].

The last 2 OP samplings (February and April, 1983) were, however, examined in the KNP using sucking mice (Gainaru, Thomson, Bengis, Esterhuysen, Bruce & Pini, 1986).

RESULTS

Buffalo cows

The viruses isolated from OP specimens of the buffalo cows at the start of the observation period, 12 months later and at the end of the study period are shown in Table 1 together with the neutralizing antibody titres determined on the former 2 occasions. At the start of the investigation viruses representative of all 3 SAT virus types were isolated from 6 of the 10 buffalo. However, a year later it was only possible to isolate virus from 2 cows (SAT 3 in both cases) and after 15 months only 1 was still positive (Table 1).

In none of the specimens from which virus was isolated was the quantity sufficient to allow titration, i.e. the viruses were present in low concentrations.

The only serum antibody titres which showed significant increase ($\geq 10^{0,6}$) between the 2 samplings were those from cows 3 (SAT 2) and 12 (SAT 3) (Table 1).

Buffalo calves

At no stage did any of the calves show clinical evidence of FMD infection and serum collections tested from the time the calves were ≥ 6 weeks of age showed only a consistent fall against all 3 SAT types (Table 2). There was thus no indication of infection in the buffalo calves. For at least the last 5 months of the observation period a majority of the calves were probably susceptible to all 3 SAT virus types, i.e. they had serum titres $\leq 10^{1,2}$.

TABLE 2 Sequential serum antibody titres to SAT 1, 2 and 3 types in buffalo calves over an 11 month period

Buffalo calf No.[1]	4/5/82[2]			17/6/82			27/7/82			10/9/82			5/10/82			22/10/82			10/11/82			8/2/83			21/4/82		
	1*	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
1	1,8	≥2,0	2,3	1,2	1,7	1,7	1,0	1,7	1,5	—	1,2	—	—	1,3	—	—	1,2	—	—	1,2	—	—	—	—	—	—	—
2	1,3	1,7	1,8	—	1,3	1,3	—	1,3	1,5	—	1,3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3	2,0	≥2,0	2,3	1,5	≥2,0	2,1	1,2	1,8	2,0	—	1,7	1,7	—	1,3	1,3	—	1,3	1,7	—	1,3	1,5	—	—	—	—	—	—
4	1,8	≥2,0	2,0	1,8	1,7	1,7	1,7	1,2	1,8	1,3	1,2	—	1,2	—	—	—	—	—	—	1,3	—	—	—	—	—	—	—
5	2,3	≥2,0	2,0	N	N	N	D																				↑
6	2,0	1,7	2,0	1,3	1,3	2,0	1,3	1,3	1,7	—	—	—	—	—	—	—	—	1,3	—	1,4	—	—	—	—	—	—	—
7	D			N	N	N																					↑
8	2,0	1,8	1,8	N	N	N	—	1,5	1,7	—	—	—	—	—	—	—	1,3	—	—	—	—	—	—	—	—	—	—
9	D																										↑

(1) Birth date shown in Table 1
(2) Date on which the animals were bled

* —SAT 1
— —SVN titre ≤1,1

A,B,C & D — Pens
⬚ — Covered stall
⬚ — Common hay rack .
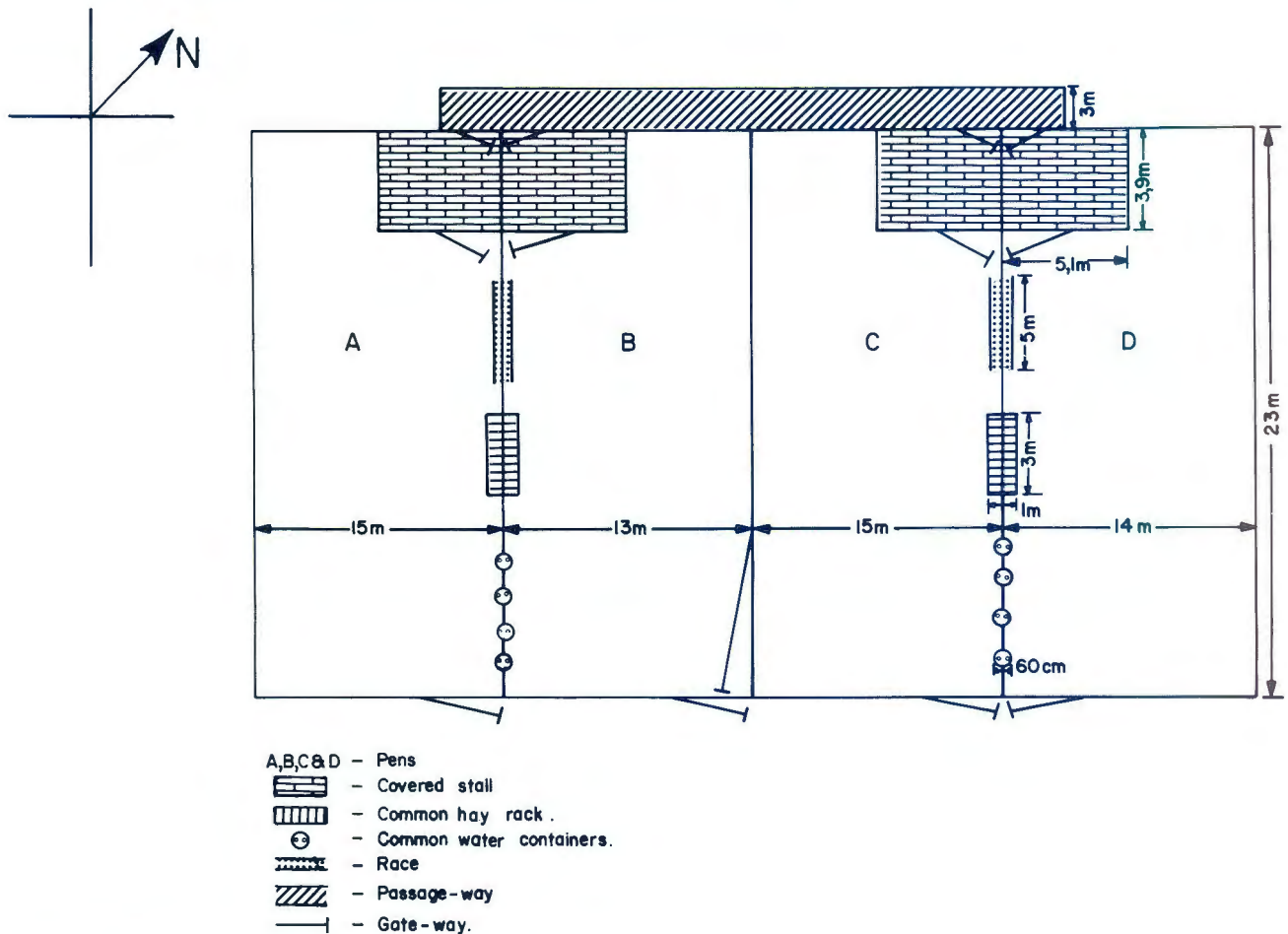⊖ — Common water containers.
✕✕✕✕ — Race
▨ — Passage-way
———┤ — Gate-way.

FIG. 1 The ground plan of the animal holding pens at Skukuza

Cattle

None of the 6 cattle showed any clinical or sereological (SN titres > $10^{1,5}$) evicence of FMD infection. Sera from the following dates were tested; July, 1982, September, 1982, October, 1982, February, 1983 and April, 1983 (results not shown).

DISCUSSION

That a group of 6 buffalo cows, shown to be carriers of FMD virus, failed to transmit the infection to their calves negated to a large extent the primary objective of this investigation which was to ascertain whether buffalo calves, in the acute stages of infection, are likely to provide a source of infection for cattle in the immediate vicinity. This necessitated the approach described in the following paper.

Why the buffalo calves failed to become infected is difficult to rationalise in the light of previous findings (Condy & Hedger, 1974). It is possible that since all the cows had only minimal amounts of virus in their pharyngeal specimens, unlike animals within 6 months of infection (Anderson *et al.*, 1979; Young, Hedger & Howell, 1972), the period between last infection and this investigation was long enough to have allowed virus levels in the OP secretions of the cows to decline to non-infectious levels.

Furthermore, despite the finding of Hedger & Condy (1985) that transmission of SAT 3 from buffalo to cattle occurred several years after infection of the buffalo, the failure of buffalo, infected only 1 month previously, to transmit SAT 2 to cattle in intimate contact with them

(Gainaru *et al.*, 1986) as well as other unsuccessful transmission experiments (Condy & Hedger, 1974; Anderson *et al.*, 1979, this investigation) indicates that, even soon after infection, carriers are generally inefficient transmitters. To what extent differences between SAT viruses affect carrier transmission is unknown.

Because carrier buffalo are apparently inefficient transmitters to their own calves it may be that infection of calves from carrier dams is a relatively rare event and that FMD virus in buffalo herds is maintained largely as a typical "childhood" infection. Certainly, a limited number of calves captured with their dams provided no evidence for transmission from cow to calf (Hedger, 1976b) while, conversely, acutely infected buffalo transmit the infection efficiently to susceptible buffalo in direct contact with them (Gainaru *et al.*, 1986). This is an aspect in need of further investigation.

Although this investigation took place during a time of severe drought, i.e. when the climatic conditions were hot as well as dry, meteorological data from the KNP has shown that, at night, temperatures and relative humidity, especially during winter months, are generally favourable to FMD virus survival in aerosols (Gainaru *et al.*, 1986).

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