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Rabies in southern Africa

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ABSTRACT

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The first confirmed outbreak of rabies in Africa, believed to have followed the importation of an infected dog from England in 1892, occurred in the eastern Cape Province of South Africa, and was brought under control in 1894. An unconfirmed epidemic of rabies in dogs occurred in western Zambia in 1901. By the following year the disease had apparently spread along a major trade route, to cause an outbreak in Zimbabwe which engulfed most of the country before being eradicated in 1913. The existence of endemic rabies of viverrids (mongooses and genets) was confirmed in South Africa in 1928, and since then the viverrid disease has continued to occur widely on the interior plateau of the country with spill-over of infection to cattle and a variety of other animals. From about 1947 onwards, an invasive form of dog rabies spread from southern Zambia and/or Angola into Namibia, across northern and eastern Botswana into Zimbabwe and the northern Transvaal by 1950, entered Mozambique in 1952, and spread from there to Swaziland in 1954. Dog rabies extended from southern Mozambique into Natal in 1961 to cause a major epidemic which was brought under control in 1968. The disease re-entered northern Natal from Mozambique in 1976 and since then dog rabies has proved difficult to control in the peri-urban settlements of Natal-KwaZulu. The disease spread from Natal to Lesotho in 1982, and into the Transkei region of the eastern Cape Province in 1987, to reach the Ciskei by 1990. The spread of the disease in dogs was followed by the emergence of rabies of jackals and cattle in central Namibia, northern Botswana, Zimbabwe and the northern Transvaal. A unique outbreak of rabies in kudu antelope occurred in central Namibia from 1977 to 1985, apparently involving oral spread of infection between individuals. A few cases of rabies in the bat-eared fox were recognized each year in Namibia from 1967 onwards, and from the 1970s the occurrence of the disease in the fox has emerged as a distinct problem in the northern Cape Province and spread to the west coast. The rabies-related viruses, Lagos bat, Mokola and Duvenhage, associated with bats, shrews and rodents in Africa, are known to have caused isolated cases of disease in South Africa, and on one occasion a small outbreak involving six cats and a dog in Bulawayo, Zimbabwe. However, the results of monoclonal antibody tests on numerous specimens indicate that the rabies-related viruses are not a major cause of disease in southern Africa.

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INTRODUCTION

Rabies (*rabidus*, L. = mad) is a highly fatal nervous disease of humans and all other warm-blooded vertebrates, caused by a virus which is present in saliva late in infection and which is generally transmitted by the bite of diseased animals, most commonly dogs and other carnivores. The causative agent of the disease is a member of the Rhabdoviridae family of rod or bullet-shaped viruses (*rhabdos*, Gr. = rod), which have a single-stranded, negative-sense RNA genome (complementary to mRNA). Within the family,

rabies virus is placed in the genus *Lyssavirus* (*lyssa*, Gr. = rage or fury), while the family also includes the *Ephemerovirus* (bovine ephemeral fever and related viruses) and *Vesiculovirus* (vesicular stomatitis and related viruses) genera of animal viruses, plus certain viruses of fishes, invertebrates, and plants (Calisher, Karabatsos, Zeller, Digoutte, Tesh, Shope, Travassos Da Rosa & St George 1989; Anonymous 1993). The lyssaviruses include rabies virus (designated lyssavirus serotype 1) and the so-called rabies-related viruses, Lagos bat, Mokola and Duvenhage (lyssavirus serotypes 2, 3 and 4) which are associated with bats, shrews and rodents in Africa, plus seven other viruses which are of unknown veterinary or medical significance (Calisher *et al.* 1989). Rabies-related viruses have also been isolated from bats in Europe, and these have been provisionally designated European bat lyssaviruses 1 (EBL 1) and 2 (EBL 2), but it is as yet uncertain whether these are to be regarded as subtypes of Duvenhage virus or recognized as separate serotypes (King 1991). It should be noted that despite early reports to the contrary, infection of bats with rabies virus proper (lyssavirus 1) has been confirmed only in the Americas, where the disease occurs in both non-haematophagous and vampire bats (Baer 1975a; 1975b; Beran 1981; Smith & Baer 1988).

It is of great epidemiological significance that recent monoclonal antibody and nucleic acid studies have shown that strains of rabies virus (lyssavirus 1) which circulate in particular host species within given geographic regions, tend to undergo genetic adaptation, resulting in the development of so-called biotypes, with subtle changes in antigenicity and pathogenicity (Wiktor & Koprowski 1978; Wiktor, Flamand & Koprowski 1980; Blancou 1988a; Smith & Baer 1988; Smith 1989; Sacramento, Bourhy & Tordo 1991; Smith, Fishbein, Rupprecht & Clark 1991). The biotypes are uniquely adapted to circulate in specific animals, so that within an affected area the disease is manifested predominantly by a single host species, or less commonly more than one, and this same host appears to be responsible for maintenance and spread of the virus; disease in other animals represents spill-over of infection resulting from sporadic contact with the major host species (Smith & Baer 1988; Smith 1989).

Rabies is widely distributed in the world, with only certain countries, mainly islands and peninsulas, being historically free of the disease or having succeeded in eradicating it in recent times (Blancou 1988b; WHO 1989; 1991). It is estimated that there are at least 25 000 human cases of the disease each year, over 90 % of which result from transmission by dogs (Fernandes & Arambulo 1985; Bögel & Motschwiller 1986). The developed nations of western Europe and North America have succeeded in drastically reducing the occurrence of the disease in dogs (urban rabies) over the past four decades, but ironically they have experienced a marked increase in the disease of wild vertebrates (sylvatic rabies) over the same period (Smith & Baer 1988; Blancou 1988b; WHO 1991). Dog rabies predominates in most of the developing nations of Central and South America, Asia and Africa, and human disease is rife. Sylvatic rabies, on the other hand, is recorded relatively infrequently in most of the developing nations, and this is ascribed partly to deficient monitoring of the disease in wild vertebrates.

Largely as a result of lack of resources, the occurrence of sociopolitical upheavals, and the existence of other national priorities, rabies appears to be least well monitored in the continent of Africa (Blancou 1988b; WHO 1991; Swanepoel 1994). The disease has been present in North Africa since antiquity, where it occurs principally as urban rabies (Blancou 1988b). In sub-Saharan Africa, where humans and other animals are more widely distributed than in northern Africa, there has been a greater tendency for epidemics of dog rabies to spread over large areas and for the disease to be observed in domestic herbivores and wild vertebrates (Blancou 1988b). This trend is most noticeable in the more developed countries of southernmost Africa, where the high proportions of cases recorded in wild animals must to some extent reflect more intensive monitoring of the disease. Nevertheless, it is clear from the history of the disease in the sub-continent (Swanepoel 1994), presented here in abbreviated form, that southern Africa has a unique blend of urban and sylvatic rabies.

ZAMBIA AND ANGOLA

Rabies was apparently present in Zambia during the 19th century, and in 1901 Chief Lewanika of the Barotse in the west of the country ordered the destruction of all dogs in the area in an attempt to control a severe outbreak of the disease (Edmonds 1922; Snyman 1940; Shone 1962). The diagnosis of the disease was first confirmed in 1913 and rabies has continued to occur throughout the country (Zyambo, Sinyangwe & Bussein 1985; Tuchili 1988; Sinyangwe 1992). The disease affects mainly dogs, but appreciable numbers of cattle are affected in the south-central part of the country, particularly in locations where jackal rabies is diagnosed close to nature reserves (Zyambo *et al.* 1985). Rabies was first confirmed in Angola in 1929 and since then the disease has been diagnosed mainly in dogs, with very few cases being recorded in other domestic or wild animals (Duarte, Rosliacov, Nsalambi & Gomes 1985), but protracted civil war in the country has hampered monitoring and control of the disease over the past few decades.

NAMIBIA

An outbreak of disease fitting the description of rabies and involving dogs, cattle and small livestock was apparently observed in Namibia in 1887 (Schneider 1985; Hübschle 1988), and from 1925 onwards there were sporadic reports of outbreaks of disease involving dogs, humans and, on one occasion a hyena, in the Ovambo, Kavango and Caprivi Strip districts in the north, bordering Angola and Zambia, with an isolated case being recorded further south in a child bitten by a dog in Swakopmund in 1928 and another in a woman bitten by a wild cat in Grootfontein in 1937 (Von Maltitz 1950). A diagnosis of rabies was finally confirmed in a dog from Rundu in Kavango in 1938, but a suspected outbreak of the disease which occurred on farms in the Gibeon and Marienthal districts in the south in 1945 could not be confirmed (Von Maltitz 1950). The position changed sharply with the occurrence of the second confirmed case of rabies in 1947, also in a dog in Rundu, which was followed in 1948 by the appearance of the disease south of the Etosha National Park in cattle in Outjou district, whence spread of disease involving black-backed jackals (*Canis mesomelas*) and cattle continued southwards to reach Otjiwarongo in 1949 and the central districts of Gobabis and Windhoek by 1951 (Onderstepoort Veterinary Institute [OVI] 1932–1992, unpublished records; Von Maltitz 1950; Alexander 1952; Schneider 1985). From 1967 onwards a few cases of the disease, less than ten, were recorded regularly each year in bat-eared foxes (*Otocyon megalotis*) (OVI 1932–1992, unpublished records). Rabies has remained a problem in Namibia, with dog and human cases being recorded mainly in the north where the density of the rural population is greatest, jackal and cattle rabies dominating in the central ranching area, and sporadic disease being associated mainly with felids (African wild cats and caracals) and viverrids (genets and mongooses) in the sheep-rearing areas of the south (OVI 1932–1992, unpublished records; Schneider 1985; Depner 1992).

An unusual development in Namibia involved epidemic spread of rabies in kudu antelope (*Tragelaphus strepsiceros*) from 1977 to 1985 in the central ranching area. A localized outbreak of rabies in kudus occurred in Windhoek district in 1975, but the epidemic which followed began in Okahandja district in 1977 and over the next few years spread to Karibib, Omaruru, Windhoek, Otavi, Otjiwarongo, Outjou, Gobabis, Grootfontein and Tsumeb districts, causing an estimated loss of 30 000–50 000 antelope, or 20 % of the population, by the time the outbreak subsided in 1985 (Shaw 1980; Barnard & Hassel 1981; Barnard, Hassel, Geyer & De Koker 1982; Hassel 1982; Schneider 1985; Hübschle 1988). It is believed that the kudu population had attained an unprecedented density during the 15 years preceding the epidemic, and this was ascribed largely to the conservation of the antelope because of the increasing value of trophy hunting and export of venison, and the occurrence of a succession of seasons of above average rainfall. An increase in jackal rabies was noted prior to the epidemic and it was surmised that rabid jackals initiated the infection in the kudus, but thereafter the number of cases recorded in the antelope was disproportionately high in comparison to that in jackals, suggesting that the disease was also transmitted directly between kudus. This possibility was strengthened by the fact that eastwards extension of the outbreak was initially checked for two years by a game control fence which hindered the passage of antelope but not small carnivores.

It is believed that transmission between kudus was favoured by their propensity to indulge in self and mutual grooming, and by the fact that oral transmission would have been facilitated by the mouth injuries which kudus sustain when browsing on the *Acacia* thorn trees which predominate in the affected area. However, individuals sometimes browse in close proximity to each other, so that transmission of infection through contamination of vegetation was possible. It was shown that kudus are highly susceptible to infection by the oral route, and that infected individuals excrete high concentrations of rabies virus in saliva (Barnard *et al.* 1982).

The start of the epidemic in kudus was followed by the occurrence of an outbreak of rabies in the Etosha National Park in the early 1980s, involving carnivores ranging from bat-eared foxes and jackals to lions. The Etosha National Park lies in the pathway of the southwards spread of rabies in 1948 and cases of the disease had been recorded there prior to 1980, but it is believed that the infection was probably re-introduced from Tsumeb district in the 1980s by jackals which are able to penetrate the game-proof fence of the park (Basson 1992).

The total cases of rabies confirmed in Namibia from 1938–1992 are summarized in Table 1 (OVI 1932–1992, unpublished records; Schneider 1985; Depner 1992; Central Veterinary Laboratory 1992a, unpublished records).

BOTSWANA

In Botswana, there were unconfirmed focal outbreaks of rabies in Lobatse in the south-east in 1919 and 1922, and in Ngamiland district in the north-west in 1936, where the diagnosis was first confirmed in a dog in 1938 according to laboratory records (Cluver 1927; OVI 1932–1992, unpublished records; Depner 1992; Snyman 1940; Henning 1956; Mansvelt 1956). From unpublished veterinary correspondence and records (Foggin 1988; Tremlett 1993), it appears that an outbreak of dog rabies of more serious proportions was noted in Ngamiland adjacent to the Caprivi Strip and Kavango districts of Namibia, at some

TABLE 1 Total confirmed cases of infection with rabies and rabies-related viruses recorded in four countries of southern Africa. Modified and updated from Swanepoel (1994). Sources of information as cited in text

Species		South Africa	Namibia	Botswana	Zimbabwe
		1928–1992	1938–1992	1938–1992	1950–1992
Wild animals					
Cynictis penicillata	Yellow mongoose	2 119	–	–	–
Unspecified mongooses		1 300[a]	16[a]	15[a]	55[b]
Galerella sanguinea	Slender mongoose	18	1	–	39
Galerella purverulenta	Small grey mongoose	38	–	–	–
Herpestes ichneumon	Large grey mongoose	–	–	–	3
Mungos mungo	Banded mongoose	4	1	–	–
Atilax paludinosus	Water mongoose	13	–	–	1
Paracynictis selousi	Selous' mongoose	1	–	–	–
Helogale parvula	Dwarf mongoose	1	–	–	–
Ichneumia albicauda	White-tailed mongoose	2	–	–	6
Suricata suricatta	Suricate	118	4	–	–
Civettictis civetta	Civet	3	–	–	29
Genetta genetta	Small-spotted genet	174	23	22	3
Mellivora capensis	Honey badger	23	27	16	45
Ictonyx striatus	Striped polecat	67[c]	2	–	5
Poecilogale albinucha	Striped weasel	1	–	–	–
Unspecified otter species		1	–	–	–
Panthera leo	Lion	–	4	–	–
Panthera pardus	Leopard	–	2	1	2
Acinonyx jubatus	Cheetah	–	4	–	–
Felis lybica	African wildcat	14	15	–	6
Felis caracal	Caracal	14	4	1	–
Felis serval	Serval	–	–	1	3
Felis nigripes	Small-spotted cat	3	–	1	–
Unspecified felids		170[d]	47[d]	12[d]	–
Canis mesomelas	Black-backed jackal	230[e]	360	193	1 595[f]
Canis adustus	Side-striped jackal	–	–	–	166
Otocyon megalotis	Bat-eared fox	273	67	6	2
Lycaon pictus	Wild dog	–	1	–	3[g]
Vulpes chama	Cape fox	9	8	–	–
Proteles cristatus	Aardwolf	23	14	–	6
Hyaena brunnea	Brown hyaena	1	2	–	–
Crocuta crocuta	Spotted hyaena	1	–	4	6
Hystrix africaeaustralis	Porcupine	–	1	–	–
Xerus inauris	Ground squirrel	32	1	–	–
Paraxerus cepapi	Tree squirrel	1	–	–	–
Thryonomys swinderianus	Greater canerat	2	–	–	–
Lepus saxatilis	Scrub hare	1	–	–	–
Orycteropus afer	Antbear	–	–	–	2
Procavia capensis	Cape hyrax	8	–	–	1
Papio ursinus	Chacma baboon	1	–	–	2
Cercopithecus aethiops	Vervet monkey	–	1	–	2
Galago moholi	Lesser bushbaby	–	1	–	–
Phacochoerus aethiopicus	Warthog	1	–	–	–
Sylvicapra grimmia	Duiker	17	9	5	7
Raphicerus campestris	Steenbok	4	1	–	–
Tragelaphus strepsiceros	Kudu	3	386	1	2
Taurotragus oryx	Eland	1	17	–	4
Hippotragus niger	Sable	–	–	–	2
Alcelaphus buselaphus	Red hartebeest	–	1	–	–
Damaliscus dorcas phillipsi	Blesbuck	1	–	–	–
Redunca arundinum	Reedbuck	1	–	–	1
Antidorcus marsupialis	Springbok	3	1	–	–
Equus burchelli	Burchell's zebra	2	–	–	–
Unspecified herbivores		6	–	1	–
Epomophorus wanlbergi	Epauletted fruit bat	14[h]	–	–	–
Nycteris thebaica	Slit-faced bat	1	–	–	1
Unidentified chiropterid, possibly *Miniopterus schreibersii*		1[i]	–	–	–
Unidentified chiropterid	Insectivorous bat	1			
Unspecified/unidentified		32[j]	2	–	–
Total wild animals		**4 754**	**1 023**	**279**	**1 999**

TABLE 1 (*continued*)

Country	South Africa	Namibia	Botswana	Zimbabwe
Period	1928–1992	1938–1992	1938–1992	1950–1992
Domestic animals				
Dogs	3 720	642	640	4 063
Cats	454	70	21	152
Cattle	2 332	1 472	761	1 567
Sheep	127	65	7	81
Goats	75	76	264	89
Horses and donkeys	58	28	42	79
Pigs	25	2	–	17
Water buffalo	–	1	–	–
Guinea pigs	1	–	–	–
Total domestic animals	**6 792**	**2 355**	**1 735**	**6 048**
Total	**11 546**	**3 378**	**2 014**	**8 047**
Humans	**307**	**12**	**32**	**159**

[a] Believed to be mainly *C. penicillata*
[b] Believed to be mainly *G. sanquinea*
[c] Probably includes some *P. albinucha*
[d] Believed to be mainly *F. lybica*
[e] Possibly includes a few *C. adustus* in north-eastern Transvaal
[f] Probably includes many *C. adustus*
[g] Captive animals
[h] Only two bats positively identified as *E. wahlbergi*
[i] Possible identity based on circumstantial evidence
[j] Probably includes domestic animals

stage before March 1950, and by September the disease had crossed to Serowe in the east and swept down the eastern border to the south of the country, i.e. infection spread to all areas where the human, and therefore dog, population was most dense. Along the way, the infection spread into south-western Zimbabwe and the northern Transvaal region of South Africa. The disease has remained active in all of the areas of Botswana initially affected, but in addition to the original problem of dog rabies with occasional human cases, there has been a tendency for increasing numbers of jackals, cattle and other livestock to be involved (Maganu & Staugard 1985; Mosienyane 1988; Masupu 1992; Tremlett 1993).

From about 1980 onwards a separate outbreak of rabies involving domestic herbivores and wild animals developed in the Ghanzi district on the western border of Botswana, apparently as an extension of the kudu epidemic in Namibia, and within a few years had spread 1 000 km south-eastwards across the country to Kgatleng district on the Transvaal border of South Africa (Mosienyane 1988). Southward extension occurred into Kgalagadi district (Mosienyane 1988), where the Gemsbok National Park of Botswana adjoins the Kalahari Gemsbok National Park of South Africa, with which it is managed as a unit, and in 1986 rabies was diagnosed in the spotted hyaena (*Crocuta crocuta*) in the South African park (OVI 1932–1992, unpublished records).

The total cases of rabies confirmed in Botswana from 1938–1992 are summarised in Table 1 (OVI 1932–1992, unpublished records; Maganu & Staugard 1985; Mosienyane 1988; Masupu 1992; Tremlett 1993). It should be noted that there are discrepancies with the figures presented by Swanepoel (1994); in particular, species identities have been published for animals previously recorded as unspecified (Tremlett 1993).

ZIMBABWE

Zimbabwe was apparently free of rabies in 1890 when European colonists arrived in the country, but some of the older indigenous inhabitants could recall that the disease had been present in their young days (Edmonds 1922). In 1902, dog rabies appeared in the Bulawayo area in south-western Zimbabwe, and there appears to be little doubt that the disease was introduced from western Zambia where the disease was known to be rampant in the Barotseland area in 1901 (there was considerable traffic between these regions along the major trade route linking the two countries at the time) (Edmonds 1922; Shone 1962). Within two years 60 000 dogs were destroyed in an attempt to control the disease in Zimbabwe, and, although this must have represented a considerable proportion of the population at the time, the disease continued to spread throughout most of the country. Control of the disease was finally achieved in 1913, this being ascribed largely to the imposition of a dog tax, which provoked drastic voluntary reduction of the population on the part of dog owners (Edmonds 1922; Shone 1962). The infection apparently did not become established in wild hosts, and failure of the outbreak to extend into South Africa was ascribed to preventive action in the form of a

radical reduction of the dog population within an 80 km wide strip of the Transvaal along the Limpopo river where it forms the northern borders of the country with Zimbabwe and Botswana (Mansvelt 1956).

After 1913, Zimbabwe remained free of rabies until 1938, when two cases were diagnosed in dogs at Victoria Falls, and, as before, the evidence indicated that the infection had been introduced from Zambia (Shone 1962). Except for bridges at certain points, the Zambezi river and the present day Lake Kariba form an effective natural barrier to the spread of rabies from Zambia, and after 1938 Zimbabwe again remained free of the disease until dog rabies crossed the south-western and southern borders of the country from Botswana and the Transvaal in 1950—it is believed that the virus was introduced by dogs which accompanied people who crossed the borders illegally to purchase grain (Adamson 1954; Shone 1962). The disease spread rapidly through Zimbabwe, following routes along the more densely populated communal farming areas, and by 1954 had reached the north of the country (Adamson 1954; Shone 1962). The growth in the human population since 1913 made it difficult to enforce formerly effective control measures, such as dog "tie-up" orders and the destruction of strays, and from 1951 onwards mass immunization campaigns were conducted with Flury LEP (low egg passage) vaccine, which had only recently become available (Adamson 1954; Shone 1962; Williamson 1976).

By the early 1960s control of the disease had been achieved over most of Zimbabwe, apart from resistant foci on the eastern and western borders with Mozambique and Botswana, and vaccination campaigns were scaled down (Mackinnon 1963; Williamson 1976; Foggin 1988). From 1965 onwards, however, political unrest culminating in civil war rendered it increasingly difficult to immunize dogs in the communal farming areas, and the incidence of rabies progressively rose to a record level of 861 confirmed cases in 1981, after the cessation of the war in 1980 (Swanepoel & Foggin 1978; Lawrence, Foggin & Norval 1980; Foggin & Swanepoel 1985; Foggin 1988). Following the formal ending of the war, the control of dog rabies was complicated by continued strife in Matabeleland in the south-west, and by an influx of refugees from the civil war in Mozambique in the east, while elsewhere in the country jackal rabies assumed serious proportions (Foggin 1988). Dogs, jackals and cattle comprise 91,8% (7 391/8 047) of all animals in which rabies was confirmed in Zimbabwe from 1950 to 1992 inclusive (Table 1) (Foggin 1988; Bingham 1992; Veterinary Research Laboratory 1992b, Zimbabwe, unpublished records) and no other country has recorded as many cases of jackal rabies.

A minor portion of the land in Zimbabwe is devoted to national parks and urban development, while the bulk of the country is divided approximately equally between commercial and communal farming. Commercial farms are generally well wooded, and apart from large wild carnivores and herbivores which have been eliminated, wildlife, including jackals, is generally preserved or tolerated, and few dogs are kept (Foggin 1988). In contrast, communal farming areas are generally overgrazed and deforested, wildlife is scarce, and dogs are kept for hunting. Consequently, dog rabies has occurred mainly in or close to communal farming areas, and jackal rabies has occurred almost exclusively on commercial farms (Foggin 1988). Both the black-backed jackal and the side-striped jackal (*C. adustus*) occur in Zimbabwe, with partially overlapping distributions, and both are involved in outbreaks of rabies.

Jackal rabies was first diagnosed in Zimbabwe in 1952, some 15 months after the disease had entered the country in 1950, and the first outbreaks occurred along the eastern border (Cumming 1982; Foggin 1985a; 1988). Thereafter, outbreaks of jackal rabies occurred in widely separated districts at irregular intervals of many years (Cumming 1982; Foggin 1988: Kennedy 1988). Since the outbreaks always appeared to occur in proximity to outbreaks of dog rabies and did not recur in the same areas for periods of seven years or more, it was argued that the virus was not adapted for maintenance in jackals but had to be re-introduced by dogs (Cumming 1982). However, several of the outbreaks which have occurred since 1965, and sporadic isolations of the virus from jackals, have taken place well away from known centres of infection in other species (Foggin 1988). Moreover, in one particular instance it was clear that an outbreak of rabies in dogs in fact followed spread of the disease in jackals (Kennedy 1988). It can therefore be concluded that rabies appears to be readily transmitted by jackals in Zimbabwe, and that the infection is freely communicable between dogs and jackals, as seems to be the case in other parts of southern Africa. An alternative explanation given for the failure of rabies to persist in circumscribed areas of commercial farming where epidemics occurred in jackals, was that the disease reduced the density of jackals in these areas to below the threshold required for the spread of the infection (Foggin 1988).

As observed in parts of Zambia, Namibia, Botswana and South Africa where jackal rabies occurs, outbreaks of the disease in jackals in Zimbabwe are invariably accompanied by the occurrence of the disease in cattle, but the reported degree of involvement of cattle varies: it is a common finding in southern Africa that laboratory confirmation of the diagnosis is sought in only a minor proportion of suspected cases of rabies in cattle, particularly once the diagnosis has already been established in a herd (Von Maltitz 1950; Brückner, Hurter & Boshoff 1978; Maganu & Staugard 1985; Zyambo *et al.* 1985; Foggin

1985a; 1988; Mosienyane 1988). In one outbreak in Zimbabwe it was established by retrospective investigation that 1 200 cattle had died, of which 140 were confirmed to have been rabid (Foggin 1988). As with cattle, the occurrence of rabies in most other species in Zimbabwe appears to represent spill-over of infection from either dogs or jackals, but there have been clusters of cases of the disease in the slender mongoose (*Galerella sanguinea*) in the south-west of the country on occasion, which suggests the existence of an independent cycle of transmission in this species (Foggin 1988).

SOUTH AFRICA, MOZAMBIQUE AND SWAZILAND

There are historical reports extending back to the eighteenth century of sporadic cases of disease resembling rabies in dogs and humans having been observed in South Africa (Cluver 1927; Neitz & Marais 1932; Snyman 1940; Henning 1956). However, an outbreak of the disease in dogs was first confirmed in the eastern Cape Province in 1893 by inoculation of rabbits, and this represents the first occasion on which a diagnosis of rabies was confirmed on the continent of Africa (Hutcheon 1894). The outbreak was initially recognized in Port Elizabeth in April 1893, but the results of inquiries suggested that the first case had occurred in September 1892 in a dog imported from England, which had become rabid a few weeks after its arrival. The outbreak was believed to have affected about 90 dogs, seven cats and a few cattle, but no wild animals, and had spread to Uitenhage, Jansenville, Willowmore and Albany districts by the time that it was brought under control in August 1894, through the muzzling and restriction of dogs and the destruction of strays (Hutcheon 1894; Eddington 1895; Henning 1956).

After 1894, rabies was not confirmed again in South Africa for 34 years, but there was mounting anecdotal evidence to indicate that an endemic form of the disease associated with viverrids was present. In particular, there was a general belief in the eastern and northern Cape Province that bites from genets caused fatal, rabies-like illness in humans, and specific reports of such incidents dated back to 1885 (Fitzsimmons 1919; Cluver 1927; Snyman 1940; Nelson 1962). Cluver (1927) documented 11 unconfirmed cases of human rabies (frequently misquoted as ten cases) which occurred in the southern Transvaal, Orange Free State and northern Cape Province from 1916 to 1927, following bites by yellow mongooses (*Cynictis penicillata*), dogs and a small-spotted genet (*Genetta genetta*). The disease was finally confirmed in 1928 in two children bitten by a yellow mongoose in Wolmaransstad district in the south-western Transvaal (Herzenberg 1928), and since that time rabies has been diagnosed regularly in South Africa.

Within a short period after the diagnosis of the disease was confirmed in 1928, rabies was recognized in numerous locations in South Africa in dogs, domestic cats, yellow mongooses, suricates (*Suricata suricatta*), genets and wild felids, and in humans and farm animals which had been bitten by these carnivores (Du Toit 1929; Neitz & Marais 1932; Neitz & Thomas 1933; 1934; Snyman 1937). Initial conjecture that the disease might have arisen by extension from the epidemics of dog rabies which had occurred in the eastern Cape Province from 1892 to 1894 and in Zimbabwe from 1902 to 1913, gave way to the conviction that rabies had long been present in viverrids in South Africa, possibly for centuries, but had simply not been recognized (Du Toit 1929; Neitz & Marais 1932; Neitz & Thomas 1933; 1934; Du Toit 1936; Snyman 1937; 1940).

The veterinary investigators were well aware that the newly recognized disease in South Africa, which occurred principally in the yellow mongoose, differed fundamentally from what they termed classical European type dog rabies in that there were sporadic cases in dogs, but no real tendency for the infection to spread among them. In fact, Neitz & Marais (1932) pre-empted the concept of rabies virus biotypes by several decades when they stated: "There seems to be complete adaptation [of the virus] to one family of Carnivora [Viverridae] and occasionally a domestic animal or human being is accidentally bitten and contracts the disease. There the outbreak ends in spite of the fact that conditions are being [sic] favourable for the spread of the disease ... the adaptation of the disease to one family, is surely not something which can occur in so short a period as a decade or two". Later, brief reference was made to the fact that experimentally infected mongooses were unable to transmit infection to dogs by bite, but the strain of virus, species of mongoose and numbers of animals on experiment, were not specified (Alexander 1952).

As the area known to be affected by rabies expanded, there was speculation that this was due to both recent spread and the fact that the true distribution of the disease was still being elucidated (Snyman 1940), but subsequently the results of deliberate investigations revealed that the occurrence of endemic mongoose rabies was confluent over the greater part of the interior plateau of South Africa west of the Drakensberg mountains (Meredith 1977; 1982). The only areas to be excluded were those which fell outside the distribution of the yellow mongoose—the northern Transvaal apart from a narrow central strip passing through Soutpansberg district, Natal apart from the north-eastern margin of the province, the easternmost Transkei portion of the Cape Province and a narrow coastal region extending from Port Elizabeth towards Cape Town (Meredith 1977; 1982; Smithers 1983). The mongoose occurs

less abundantly in Botswana where it is absent in the east, and it is present in Namibia apart from the coastal Namib desert (Smithers 1983).

The yellow mongoose is diurnal and its role as a maintenance host for rabies virus is facilitated by the fact that it lives in colonies (Snyman 1940; Zumpt 1968; 1969; 1976; 1982; Smithers 1983; Wenhold 1990; Raza, Wenhold, Howard, Marais, & Pallett 1992). It is most abundant in the north-western Orange Free State and in the adjacent south-western Transvaal, and mongoose rabies is most prevalent in this area (Snyman 1940; Zumpt 1976; 1982). Over much of its distribution, the yellow mongoose utilizes and adapts warrens pioneered by the ground squirrel (*Xerus inauris*), a rodent with which the mongoose shares the warrens in apparent harmony (Snyman 1940; Zumpt 1976). Itinerant groups of suricates, which are also viverrids, occasionally evict yellow mongooses and ground squirrels temporarily from warrens (Snyman 1940; Zumpt 1982). Comparatively few cases of rabies have been recorded in ground squirrels and suricates, the distributions of which largely coincide with that of the yellow mongoose, but there appear to have been no specific attempts to determine the relative population densities of the three species. It is possible that rabid ground squirrels and suricates have been misidentified as yellow mongooses on occasion, or categorized as unidentified mongooses.

As early as 1930 efforts were made to control viverrid rabies through the eradication of the yellow mongoose, and from 1939 onwards it became routine to pump cyanogas (later phosphine) into warrens in locations where mongoose rabies was diagnosed (Snyman 1940; Zumpt & De Bruyn 1967). About 50 000–160 000 hectares were treated annually until exceptionally heavy rains in 1974–1976 restricted the access of control teams to affected sites (Department of Agriculture 1940–1992, unpublished records; Snyman 1940, Zumpt & De Bruyn 1967). Since then mongoose control, which had become prohibitively expensive, has been applied much more selectively to strategic locations where the disease occurs in proximity to urban centres.

It was realized from an early stage that focal eradication of the mongoose provided only temporary control of rabies, and the incidence of the disease rose progressively in each decade from 1950 onwards to reach epidemic proportions by the early 1970s, despite the application of the control measures, and continued to fluctuate at high levels in the 1970s and 1980s following the abandonment of systematic mongoose control (Table 2) (OVI 1932–1992, unpublished records; Snyman 1940; Zumpt 1982).

Rabies of the yellow mongoose remains hyperendemic in the south-western Transvaal and adjoining north-western Orange Free State, but occurs throughout the southern Transvaal, and the Orange Free State where the mongoose constitutes approximately 60 % of all animals in which the disease has been recorded over the past two decades (OVI 1932–1992, unpublished records). There is spill-over of infection to cattle, dogs, cats, other domestic animals, the striped polecat (*Ictonyx striatus*) and the slender and water (*Atilax paludinosus*) mongooses. Sporadic cases of rabies are also recorded in suricates, genets, bat-eared foxes, jackals and wild felids, particularly in the drier western districts (OVI 1932–1992, unpublished records). Since sheep outnumber cattle in the areas where mongoose rabies occurs, and both species predispose themselves to facial bites by displaying curiosity towards rabid mongooses (Du Toit 1929; OVI 1932–1992, unpublished records; Alexander 1952; Maré 1962; Mansvelt 1965), it is curious that the number of cases of rabies recorded in cattle vastly outnumber those in sheep (Table 1).

The epidemiology of the disease is more complex in the Cape Province, where the yellow mongoose constitutes less than 30 % of rabid animals recorded over the past 20 years (OVI 1932–1992, unpublished records), and where several other carnivores appear to be involved in independent transmission of the virus. Suricates, striped polecats and ground squirrels seem to acquire the infection only where the disease occurs in the yellow mongoose, but there have been clusters of cases suggestive of localized spread in the water mongoose, and in the small grey mongoose (*Galerella purverulenta*), which occurs mainly south of the Orange River (OVI 1932–1992, unpublished records). In the northern Cape Province, rabies of genets and wild felids has been diagnosed more frequently than elsewhere in the country, but it is not clear whether there is independent circulation of virus in these animals or whether they acquire infection from mongooses, possibly in their role as predators. However, there has also been a much higher incidence of rabies in domestic cats in the same area than elsewhere (Barnard 1979a), and this could indicate that there is spread of infection among felids, with the African wild cat (*Felis lybica*) serving as a link to feral domestic cats with which it interbreeds.

There is stronger evidence to suggest that there is independent spread of rabies in the bat-eared fox, a small canid which occurs in the drier western parts of the sub-continent, and which subsists largely on termites. Sporadic cases of rabies were recorded in the fox from 1955 onwards, but an increase in the incidence of the disease was noted in the northern and western Cape Province during the 1970s, shortly after there had been a similar increase in Namibia (see above), and from 1980 onwards there have been up to 24 confirmed cases each year, with progressive spread of the disease to the west coast (almost to the environs of Cape

TABLE 2 Total confirmed cases of infection with rabies and rabies-related viruses recorded in animals in South Africa, 1928–1992. Sources of information as for Table 1

Species		28	29	30	31	32	33	34	35	36	37	38
Domestic animals												
Dogs		–	1	1	1	1	1	1	1	2	1	6
Cats		–	–	–	–	2	4	6	1	3	–	3
Cattle		–	1	3	2	2	1	1	1	7	3	16
Sheep		–	–	–	1	–	2	1	–	–	–	–
Goats		–	–	–	–	–	–	–	–	–	–	–
Horses and donkeys		–	–	–	–	–	–	–	1	–	–	3
Pigs		–	2	–	–	–	–	–	–	–	–	2
Guinea pigs		–	–	–	–	–	–	–	–	–	–	–
Total domestic animals		–	4	4	4	5	8	9	4	12	4	30
Wild animals												
Cynictis penicillata	Yellow mongoose	2	5	1	1	6	15	8	–	4	5	6
Unspecified mongooses, probably *C. penicillata*		–	–	–	–	–	–	–	–	–	–	1
Galerella sanguinea	Slender mongoose	–	–	–	–	–	–	–	–	–	–	–
Galerella purverulenta	Small grey mongoose	–	–	1	–	–	–	–	–	–	–	–
Mungos mungo	Banded mongoose	–	–	–	–	–	–	–	–	–	–	–
Atilax paludinosus	Water mongoose	–	–	–	–	–	–	–	–	–	–	–
Paracynictis selousi	Selous' mongoose	–	–	–	–	–	–	–	–	–	–	–
Helogale parvula	Dwarf mongoose	–	–	–	–	–	–	–	–	–	–	–
Ichneumia albicauda	White-tailed mongoose	–	–	–	–	–	–	–	–	–	–	–
Suricata suricatta	Suricate	–	–	2	–	1	–	–	–	–	–	–
Civettictis civetta	Civet	–	–	–	–	–	–	–	–	–	–	–
Genetta spp. mainly *G. genetta*	Small-spotted genet	–	2	–	–	3	1	–	–	2	–	1
Unspecified viverrids		–	1	–	–	–	–	–	–	–	–	–
Mellivora capensis	Honey badger	–	–	–	–	–	–	–	–	–	–	–
Ictonyx striatus	Striped polecate	–	–	–	–	–	–	–	–	–	–	–
Poecilogale albinucha	Striped weasel	–	–	–	–	–	–	–	–	–	–	–
Aonyx capensis or *Lutra maculicollis*	Otter	–	–	–	–	–	–	–	–	–	–	–
Felis lybica	African wildcat	–	–	–	–	–	–	–	–	–	–	–
Felis caracal	Caracal	–	–	–	–	–	–	–	–	–	–	–
Felis nigripes	Small-spotted cat	–	–	–	–	–	–	–	–	–	–	–
Unspecified felids		–	–	–	–	–	1	2	–	3	–	–
Canis spp. mainly *C. mesomelas*	Black-backed jackal	–	–	–	–	–	–	–	–	–	–	–
Otocyon megalotis	Bat-eared fox	–	–	–	–	–	–	–	–	–	–	–
Vulpes chama	Cape fox	–	–	–	–	–	–	–	–	–	–	–
Proteles cristatus	Aardwolf	–	–	–	–	–	–	–	–	–	–	–
Hyaena brunnea	Brown hyaena	–	–	–	–	–	–	–	–	–	–	–
Crocuta crocuta	Spotted hyaena	–	–	–	–	–	–	–	–	–	–	–
Xerus inauris	Ground squirrel	–	–	–	–	–	–	–	–	1	–	–
Paraxerus cepapi	Tree squirrel	–	–	–	–	–	–	–	–	–	–	–
Thryonomys swinderianus	Greater cane rat	–	–	–	–	–	–	–	–	–	–	–
Lepus spp., probably *L. saxatilis*	Scrub hare	–	–	–	–	–	–	–	–	–	–	–
Procavia capensis	Cape hyrax	–	–	–	–	–	–	–	–	–	–	–
Papio ursinus	Chacma baboon	–	–	–	–	–	–	–	–	–	–	–
Phacochoerus aethiopicus	Warthog	–	–	–	–	–	–	–	–	–	–	–
Sylvicapra grimmia	Duiker	–	–	–	–	–	–	–	–	–	–	–
Raphicerus campestris	Steenbok	–	–	–	–	–	–	–	–	–	–	–
Tragelaphus strepsiceros	Kudu	–	–	–	–	–	–	–	–	–	–	–
Taurotragus oryx	Eland	–	–	–	–	–	–	–	–	–	–	–
Damaliscus dorcas phillipsi	Blesbuck	–	–	–	–	–	–	–	–	–	–	–
Redunca arundinum	Reedbuck	–	–	–	–	–	–	–	–	–	–	–
Antidorcus marsupialis	Springbok	–	–	–	–	–	–	–	–	–	–	–
Equus burchelli	Zebra	–	–	–	–	–	–	–	–	–	–	–
Unspecified herbivores		–	–	–	–	–	–	–	–	–	–	–
Epomophorus wahlbergi	Wahlberg's epauletted fruit bat	–	–	–	–	–	–	–	–	–	–	–
Unspecified pteropodid, probably *E. wahlbergi*		–	–	–	–	–	–	–	–	–	–	–
Nycteris thebaica	Slit-faced bat	–	–	–	–	–	–	–	–	–	–	–
Unidentified chiropterid, possibly *Miniopterus schreibersii*		–	–	–	–	–	–	–	–	–	–	–
Unindentified chiropterid	Insectivorous bat	–	–	–	–	–	–	–	–	–	–	–
Other unspecified or unidentified animals*		–	–	–	–	–	–	–	4	–	–	–
Total wild animals		2	8	4	1	10	17	10	4	10	5	8
Total		2	12	8	5	15	25	19	8	22	9	38

* Probably includes domestic animals

TABLE 2 (*continued*)

Species		39	40	41	42	43	44/45	46	47	48	49	50
Domestic animals												
Dogs		3	2	–	5	2	3	1	2	1	4	25
Cats		–	–	1	–	1	2	3	1	1	3	1
Cattle		9	17	4	2	10	30	2	3	8	15	18
Sheep		–	2	–	1	–	1	–	–	–	–	1
Goats		1	–	–	–	–	–	–	–	–	–	
Horses and donkeys		–	–	–	1	–	–	–	–	–	1	3
Pigs		1	–	–	–	–	–	–	1		–	–
Guinea pigs		–	–	–	–	–	–	–	–		–	–
Total domestic animals		14	21	5	9	13	36	6	7	10	23	48
Wild animals												
Cynictis penicillata	Yellow mongoose	13	20	4	6	6	8	2	3	5	24	10
Unspecified mongooses, probably *C. penicillata*		2	–	–	–		–	–	–	–		
Galerella sanguinea	Slender mongoose	–	–	–	–	–	–	–		–		–
Galerella purverulenta	Small grey mongoose	–	–	–	–	–	–	–	–	–		
Mungos mungo	Banded mongoose	–	–	–	–	–		–	–			
Atilax paludinosus	Water mongoose	–	–	–	–		–	–	–		–	
Paracynictis selousi	Selous' mongoose	–	–		–	–	–		–	–		
Helogale parvula	Dwarf mongoose	–	–	–	–	–		–	–		–	–
Ichneumia albicauda	White-tailed mongoose	–	–	–	–		–	–	–		–	–
Suricata suricatta	Suricate	–	–	–	1	–	1	–	2	–	–	
Civettictis civetta	Civet	–	–	–	–	–	–			–		
Genetta spp. mainly *G. genetta*	Small-spotted genet	1	–	–	–	1	–	–	–	2	–	1
Unspecified viverrids		–	–	–	–	–	–		–	–		–
Mellivora capensis	Honey badger	–	–	–	–	–	–	–	–		–	–
Ictonyx striatus	Striped polecate	1	–	–	–	–	–	–	–	–	–	–
Poecilogale albinucha	Striped weasel	–	–	–	–	–	–	–	–			–
Aonyx capensis or *Lutra maculicollis*	Otter	–	–	–	–	–	–	–	–	–	–	
Felis lybica	African wildcat	–	–	–	–	–	4	–	–	–		–
Felis caracal	Caracal	–	–	–	–	–	–	–	–	1	–	–
Felis nigripes	Small-spotted cat	–	–	–	–	–	–	–	–	2	–	–
Unspecified felids		–	1	–	–	–	–	–	1	–	–	1
Canis spp. mainly *C. mesomelas*	Black-backed jackal	–	–	–	–	–	–	–	1		–	3
Otocyon megalotis	Bat-eared fox	–	–	–	–	–	–	–	–	–	–	
Vulpes chama	Cape fox	1	–	–	–	–	–	–	–	–	–	–
Proteles cristatus	Aardwolf	–	1	–	–	–	–	–	–	–		–
Hyaena brunnea	Brown hyaena	–	–	–	–	–	–	–	–	–	–	
Crocuta crocuta	Spotted hyaena	–	–	–	–	–	–	–	–		–	–
Xerus inauris	Ground squirrel	1	–	–	–	–	–	–	–	–	–	–
Paraxerus cepapi	Tree squirrel	–	–	–	–	–	–	–	–	–	–	–
Thryonomys swinderianus	Greater cane rat	–	–	–	–	–	–	–	–	–	–	–
Lepus spp., probably *L. saxatilis*	Scrub hare	–	–	–	–	–	–	–			–	–
Procavia capensis	Cape hyrax	–	–	–	–	–	–	–		–	–	–
Papio ursinus	Chacma baboon	–	–	–	–	–	–	–	–	–		–
Phacochoerus aethiopicus	Warthog	–	–	–	–	–	–	–	–		–	
Sylvicapra grimmia	Duiker	–	–	–	–	–		–	–	–		–
Raphicerus campestris	Steenbok	–	–	–	–	–	–	–	–	–	–	
Tragelaphus strepsiceros	Kudu	–	–	–	–	–	–	–	–		–	
Taurotragus oryx	Eland	–	–		–	–	–	–		–	–	
Damaliscus dorcas phillipsi	Blesbuck	–	–	–	–	–		–	–			–
Redunca arundinum	Reedbuck	–	–	–	–	–	–	–		–		
Antidorcus marsupialis	Springbok	–	–	–	–	–	–		–			
Equus burchelli	Zebra	–	–		–	–	–	–				
Unspecified herbivores		–	–	–	–	–	–			–		
Epomophorus wahlbergi	Wahlberg's epauletted fruit bat	–	–	–	–	–	–	–	–	–	–	–
Unspecified pteropodid, probably *E. wahlbergi*		–	–	–	–	–	–	–	–	–	–	
Nycteris thebaica	Slit-faced bat	–	–	–	–	–	–	–	–		–	–
Unidentified chiropterid, possibly *Miniopterus schreibersii*		–	–	–	–	–	–	–	–	–	–	–
Unindentified chiropterid	Insectivorous bat	–	–	–	–	–	–	–	–	–		–
Other unspecified or unidentified animals*		–	–	–	–	–	–	–	–	–	–	–
Total wild animals		19	22	4	7	7	13	2	7	10	24	15
Total		33	43	9	16	20	49	8	14	20	47	63

* Probably includes domestic animals

TABLE 2 (*continued*)

Species		51	52	53	54	55	56	57	58	59	60	61
Domestic animals												
Dogs		38	14	16	19	12	20	29	17	35	12	80
Cats		–	4	1	2	6	1	3	2	10	3	8
Cattle		–	25	21	29	23	11	22	23	14	21	48
Sheep		–	–	–	1	1	1	–	1	1	1	1
Goats		–	–	–	–	–	–	–	–	–	–	–
Horses and donkeys		–	2	–	–	–	–	–	–	1	–	–
Pigs		–	–	–	–	1	–	–	1	–	–	–
Guinea pigs		–	–	–	–	–	–	–	–	–	–	–
Total domestic animals		38	45	38	51	43	33	54	44	61	37	137
Wild animals												
Cynictis penicillata	Yellow mongoose	–	8	5	25	10	2	1	2	1	1	1
Unspecified mongooses, probably *C. penicillata*		–	–	–	1	5	5	15	18	9	18	43
Galerella sanguinea	Slender mongoose	–	–	–	–	–	–	–	–	–	–	–
Galerella purverulenta	Small grey mongoose	–	–	–	–	–	–	–	–	–	–	–
Mungos mungo	Banded mongoose	–	–	–	–	–	–	–	–	–	–	–
Atilax paludinosus	Water mongoose	–	–	–	–	–	–	–	–	–	–	–
Paracynictis selousi	Selous' mongoose	1	–	–	–	–	–	–	–	–	–	–
Helogale parvula	Dwarf mongoose	–	–	–	–	–	–		–	–	–	–
Ichneumia albicauda	White-tailed mongoose	–	–	–	–	–	–	–	–	–	–	–
Suricata suricatta	Suricate	–	–	–	–	–	–	–	–	–	–	–
Civettictis civetta	Civet	–	–	–	–	–	–	–	–	–	–	–
Genetta spp. mainly *G. genetta*	Small-spotted genet	–	3	–	1	3	1	1	1	1	1	3
Unspecified viverrids		–	–	–	–	–	–	–	–	–	–	–
Mellivora capensis	Honey badger	–	–	1	–	–	–	–	–	–	–	1
Ictonyx striatus	Striped polecate	–	–	–	–	–	–	–	–	–	–	–
Poecilogale albinucha	Striped weasel	–	–	–	–	–	–	–	–	–	–	–
Aonyx capensis or *Lutra maculicollis*	Otter	–	–	–	–	–	–	–	–	–	–	–
Felis lybica	African wildcat	–	–	–	–	–	–	–	–	–	–	–
Felis caracal	Caracal	–	–	–	–	–	–	–	–	–	–	–
Felis nigripes	Small-spotted cat	–	–	–	–	–	–	–	–	–	–	–
Unspecified felids		–	1	1	–	–	1	2	3	–	1	2
Canis spp. mainly *C. mesomelas*	Black-backed jackal	–		7	–	1	1	–	–	2	–	4
Otocyon megalotis	Bat-eared fox	–	–	–	–	1	1	–	–	–	–	–
Vulpes chama	Cape fox	–	–	–	–	–	–		–	–	–	–
Proteles cristatus	Aardwolf	–	–	–	–	–	–	–	–	–	–	–
Hyaena brunnea	Brown hyaena	–	–	–	–	–	–	–	–	–	–	–
Crocuta crocuta	Spotted hyaena	–	–	–	–	–	–	–	–	–	–	–
Xerus inauris	Ground squirrel	–	–	–	1	–	–	1	1	–	1	–
Paraxerus cepapi	Tree squirrel	–	–	–	–	–	–	–	–	–	–	–
Thryonomys swinderianus	Greater cane rat	–	–	–	–	–	–	–	–	–	–	–
Lepus spp., probably *L. saxatilis*	Scrub hare	–	–	–	–	–	–	–	–	–	–	–
Procavia capensis	Cape hyrax	–	–	–	–	–	–	–	–	–	–	1
Papio ursinus	Chacma baboon	–	–	–	–	–	–	–	–	–	–	–
Phacochoerus aethiopicus	Warthog	–	–	–	–	–	–	–	–	–	–	–
Sylvicapra grimmia	Duiker	–	–	–	–	–	–	–	–	1	1	–
Raphicerus campestris	Steenbok	–	–	–	–	–	–	–	–	–	–	–
Tragelaphus strepsiceros	Kudu	–	–	–	–	–	–	–	–	–	–	–
Taurotragus oryx	Eland	–	–	–	–	–	–	–	–	–	–	–
Damaliscus dorcas phillipsi	Blesbuck	–	–	–	–	–	–	–	–	–	–	–
Redunca arundinum	Reedbuck	–	–	–	–	–	–	–	–	–	–	–
Antidorcus marsupialis	Springbok	–	–	–	–	–	–	–	–	–	–	–
Equus burchelli	Zebra	–	–	–	–	–	–	–	–	–	–	–
Unspecified herbivores		–	–	–	–	–	–	–	–	–	–	–
Epomophorus wahlbergi	Wahlberg's epauletted fruit bat	–	–	–	–	–	–	–	–	–	–	–
Unspecified pteropodid, probably *E. wahlbergi*		–	–	–	–	–	–	–	–	–	–	–
Nycteris thebaica	Slit-faced bat	–	–	–	–	–	–	–	–	–	–	–
Unidentified chiropterid, possibly *Miniopterus schreibersii*		–	–	–	–	–	–	–	–	–	–	–
Unindentified chiropterid	Insectivorous bat	–	–	–	–	–	–	–	–	–	–	–
Other unspecified or unidentified animals*		23	–	–	–	–	–	–	2	–	–	–
Total wild animals		24	12	14	28	20	11	20	27	14	23	55
Total		62	57	52	79	63	44	74	71	75	60	192

* Probably includes domestic animals

TABLE 2 (*continued*)

Species		62	63	64	65	66	67	68	69	70	71	72
Domestic animals												
Dogs		108	68	79	140	75	60	29	16	9	20	14
Cats		21	8	15	20	7	6	18	8	8	18	11
Cattle		62	36	37	59	32	24	58	35	29	62	36
Sheep		3	1	2	1	–	1	3	1	3	4	4
Goats		1	–	–	1	1	1	–	–	–	–	–
Horses and donkeys		–	–	–	2	–	1	–	1	1	1	2
Pigs		3	1	–	–	1	1	–	1	–	–	–
Guinea pigs		–	–	–	–	–	–	–	–	–	–	–
Total domestic animals		198	114	133	223	116	94	108	62	50	105	67
Wild animals												
Cynictis penicillata	Yellow mongoose	4	–	17	76	35	40	55	29	43	152	164
Unspecified mongooses, probably *C. penicillata*		115	66	58	–	30	29	26	23	22	27	21
Galerella sanguinea	Slender mongoose	–	–	–	–	–	–	–	2	1	2	2
Galerella purverulenta	Small grey mongoose	–	–	–	–	–	–	2	–	1	3	2
Mungos mungo	Banded mongoose	–	–	–	–	–	–	–	–	–	–	–
Atilax paludinosus	Water mongoose	–	–	–	–	–	–	1	1	–	–	–
Paracynictis selousi	Selous' mongoose	–	–	–	–	–	–	–	–	–	–	–
Helogale parvula	Dwarf mongoose	–	–	–	–	–	–	–	–	–	–	–
Ichneumia albicauda	White-tailed mongoose	–	–	–	–	–	–	–	–	–	1	1
Suricata suricatta	Suricate	–	–	–	–	5	1	2	–	3	5	15
Civettictis civetta	Civet	–	–	–	–	–	–	–	–	–	–	–
Genetta spp. mainly *G. genetta*	Small-spotted genet	9	6	6	5	3	2	16	2	2	3	4
Unspecified viverrids		–	–	–	–	–	–	–	–	–	–	–
Mellivora capensis	Honey badger	1	–	–	–	–	–	–	–	–	1	–
Ictonyx striatus	Striped polecate	1	3	1	1	2	1	–	–	–	4	4
Poecilogale albinucha	Striped weasel	–	–	–	–	–	–	–	1	–	–	–
Aonyx capensis or *Lutra maculicollis*	Otter	–	–	–	–	–	–	–	–	–	–	–
Felis lybica	African wildcat	–	–	–	–	–	–	–	–	–	–	–
Felis caracal	Caracal	–	–	–	–	–	–	–	–	–	–	–
Felis nigripes	Small-spotted cat	–	–	–	–	–	–	–	–	–	–	–
Unspecified felids		4	4	4	4	4	2	12	5	9	–	7
Canis spp. mainly *C. mesomelas*	Black-backed jackal	5	1	7	3	4	2	2	1	–	3	2
Otocyon megalotis	Bat-eared fox	–	–	1	1	1	1	–	–	2	8	5
Vulpes chama	Cape fox	–	–	–	–	–	–	–	–	–	–	1
Proteles cristatus	Aardwolf	–	–	–	–	1	1	1	–	–	1	1
Hyaena brunnea	Brown hyaena	–	–	–	–	–	–	–	–	–	–	–
Crocuta crocuta	Spotted hyaena	–	–	–	–	–	–	–	–	–	–	–
Xerus inauris	Ground squirrel	–	–	–	–	1	–	–	–	–	2	3
Paraxerus cepapi	Tree squirrel	–	–	–	–	–	–	–	–	–	–	–
Thryonomys swinderianus	Greater cane rat	–	–	–	–	–	–	–	–	–	–	–
Lepus spp., probably *L. saxatilis*	Scrub hare	–	–	–	–	–	–	–	–	–	–	–
Procavia capensis	Cape hyrax	–	–	–	–	1	–	–	–	–	2	–
Papio ursinus	Chacma baboon	–	–	1	–	–	–	–	–	–	–	–
Phacochoerus aethiopicus	Warthog	–	–	–	–	–	–	–	–	–	–	–
Sylvicapra grimmia	Duiker	–	–	–	1	–	–	–	–	1	–	–
Raphicerus campestris	Steenbok	–	–	–	–	–	–	–	–	1	–	–
Tragelaphus strepsiceros	Kudu	–	–	–	–	–	–	–	–	–	–	–
Taurotragus oryx	Eland	–	–	–	–	–	–	–	–	–	–	–
Damaliscus dorcas phillipsi	Blesbuck	–	–	–	–	–	–	–	–	–	–	–
Redunca arundinum	Reedbuck	–	–	–	–	–	–	–	–	–	1	–
Antidorcus marsupialis	Springbok	–	–	–	–	–	1	1	–	–	–	–
Equus burchelli	Zebra	–	–	–	–	–	–	–	–	–	–	–
Unspecified herbivores		–	–	–	–	–	–	–	–	–	–	–
Epomophorus wahlbergi	Wahlberg's epauletted fruit bat	–	–	–	–	–	–	–	–	–	–	–
Unspecified pteropodid, probably *E. wahlbergi*		–	–	–	–	–	–	–	–	–	–	–
Nycteris thebaica	Slit-faced bat	–	1	–	–	–	–	–	–	–	–	–
Unidentified chiropterid, possibly *Miniopterus schreibersii*		–	–	–	–	–	–	–	–	–	–	–
Unindentified chiropterid	Insectivorous bat	–	–	–	–	–	–	–	–	–	–	–
Other unspecified or unidentified animals*		–	–	–	–	–	1	–	–	–	–	–
Total wild animals		139	81	95	91	87	81	118	64	85	215	232
Total		337	195	228	314	203	175	226	126	135	320	299

* Probably includes domestic animals

TABLE 2 (*continued*)

Species		73	74	75	76	77	78	79	80	81	82	83
Domestic animals												
Dogs		13	14	24	30	27	32	71	202	75	55	90
Cats		11	8	13	11	6	8	13	15	6	12	20
Cattle		62	33	76	39	51	51	79	108	64	48	83
Sheep		5	–	1	3	5	3	3	6	2	4	5
Goats		1	–	5	2	–	1	2	–	11	–	3
Horses and donkeys		–	1	–	–	3	–	–	1	1	1	2
Pigs		–	–	–	–	–	–	–	–	–	1	–
Guinea pigs		–	–	–	–	–	–	–	1	–	–	–
Total domestic animals		92	56	119	85	92	95	168	333	159	121	203
Wild animals												
Cynictis penicillata	Yellow mongoose	157	64	56	40	54	32	51	95	35	45	84
Unspecified mongooses, probably *C. penicillata*		14	5	10	9	9	21	39	52	46	50	89
Galerella sanguinea	Slender mongoose	–	1	–	–	1	–	–	–	–	–	–
Galerella pulverulenta	Small grey mongoose	3	–	–	–	–	–	–	–	–	–	1
Mungos mungo	Banded mongoose	–	1	–	–	–	–	–	–	–	–	1
Atilax paludinosus	Water mongoose	–	–	–	–	–	–	–	1	–	1	1
Paracynictis selousi	Selous' mongoose	–	–	–	–	–	–	–	–	–	–	–
Helogale parvula	Dwarf mongoose	–	–	–	–	–	–	–	–	–	–	–
Ichneumia albicauda	White-tailed mongoose	–	–	–	–	–	–	–	–	–	–	–
Suricata suricatta	Suricate	13	6	10	2	2	2	1	1	6	3	–
Civettictis civetta	Civet	–	1	–	–	–	–	–	1	–	–	1
Genetta spp. mainly *G. genetta*	Small-spotted genet	8	3	7	8	1	7	–	5	3	9	10
Unspecified viverrids		–	–	–	–	–	–	–	–	–	–	–
Mellivora capensis	Honey badger	–	–	–	1	–	–	1	4	2	–	1
Ictonyx striatus	Striped polecate	2	–	4	1	2	2	3	5	3	4	3
Poecilogale albinucha	Striped weasel	–	–	–	–	–	–	–	–	–	–	–
Aonyx capensis or *Lutra maculicollis*	Otter	–	–	–	–	–	–	–	–	–	–	–
Felis lybica	African wildcat	–	–	–	1	–	–	–	–	–	–	–
Felis caracal	Caracal	–	–	1	–	2	–	–	1	1	2	–
Felis nigripes	Small-spotted cat	–	–	–	–	–	–	–	–	–	–	–
Unspecified felids		8	3	5	1	7	12	4	3	1	8	10
Canis spp. mainly *C. mesomelas*	Black-backed jackal	1	4	4	6	4	2	15	18	4	4	4
Otocyon megalotis	Bat-eared fox	3	4	2	2	4	3	5	24	22	16	23
Vulpes chama	Cape fox	–	–	–	–	–	–	–	–	–	–	1
Proteles cristatus	Aardwolf	–	–	–	–	1	1	–	–	1	–	1
Hyaena brunnea	Brown hyaena	–	–	–	–	–	–	–	–	–	–	–
Crocuta crocuta	Spotted hyaena	–	–	–	–	–	–	–	–	–	–	–
Xerus inauris	Ground squirrel	2	1	–	2	1	2	–	2	–	–	4
Paraxerus cepapi	Tree squirrel	–	–	–	–	–	–	–	–	–	–	–
Thryonomys swinderianus	Greater cane rat	–	–	–	–	–	–	–	–	–	–	–
Lepus spp., probably *L. saxatilis*	Scrub hare	–	–	–	–	–	1	–	–	–	–	–
Procavia capensis	Cape hyrax	–	1	–	–	–	–	–	–	–	–	–
Papio ursinus	Chacma baboon	–	–	–	–	–	–	–	–	–	–	–
Phacochoerus aethiopicus	Warthog	–	–	–	–	–	–	–	–	–	–	–
Sylvicapra grimmia	Duiker	–	–	–	–	1	–	1	2	–	1	4
Raphicerus campestris	Steenbok	–	–	–	–	–	–	–	1	–	–	–
Tragelaphus strepsiceros	Kudu	–	–	1	–	–	–	1	1	–	–	–
Taurotragus oryx	Eland	–	–	–	–	–	–	–	–	–	–	–
Damaliscus dorcas phillipsi	Blesbuck	–	–	–	–	–	–	–	–	–	1	–
Redunca arundinum	Reedbuck	–	–	–	–	–	–	–	–	–	–	–
Antidorcus marsupialis	Springbok	–	–	–	–	–	–	–	–	–	–	–
Equus burchelli	Zebra	–	–	–	–	–	–	–	–	–	–	–
Unspecified herbivores		–	–	–	–	–	–	–	–	–	–	–
Epomophorus wahlbergi	Wahlberg's epauletted fruit bat	–	–	–	–	–	–	–	1	–	–	–
Unspecified pteropodid, probably *E. wahlbergi*		–	–	–	–	–	–	–	9	3	–	–
Nycteris thebaica	Slit-faced bat	–	–	–	–	–	–	–	–	–	–	–
Unidentified chiropterid, possibly *Miniopterus schreibersii*		–	–	–	–	–	–	–	–	1	–	–
Unindentified chiropterid	Insectivorous bat	–	–	–	–	–	–	–	–	–	–	–
Other unspecified or unidentified animals*		–	–	–	–	–	–	–	–	1	–	–
Total wild animals		211	94	100	73	89	85	121	226	129	144	239
Total		303	150	219	158	181	180	289	559	288	265	442

* Probably includes domestic animals

TABLE 2 (*continued*)

Species		84	85	86	87	88	89	90	91	92
Domestic animals										
Dogs		189	116	135	278	199	160	285	356	395
Cats		14	12	10	18	16	10	12	11	16
Cattle		62	57	77	117	74	81	105	81	122
Sheep		2	5	2	6	5	9	6	8	8
Goats		–	4	2	5	2	2	6	9	15
Horses and donkeys		–	–	2	4	2	2	12	2	5
Pigs		1	1	–	–	1	–	2	4	–
Guinea pigs		–	–	–	–	–	–	–	–	–
Total domestic animals		268	195	228	428	299	264	428	471	561
Wild animals										
Cynictis penicillata	Yellow mongoose	98	65	73	58	36	22	84	60	85
Unspecified mongooses, probably *C. penicillata*		57	87	89	73	27	57	–	–	28
Galerella sanguinea	Slender mongoose	–	1	1	1	1	1	–	2	2
Galerella purverulenta	Small grey mongoose	6	2	2	3	–	–	8	4	–
Mungos mungo	Banded mongoose	–	–	1	–	–	–	–	–	1
Atilax paludinosus	Water mongoose	1	2	1	1	1	–	–	–	2
Paracynictis selousi	Selous' mongoose	–	–	–	–	–	–	–	–	–
Helogale parvula	Dwarf mongoose	1	–	–	–	–	–	–	–	–
Ichneumia albicauda	White-tailed mongoose	–	–	–	–	–	–	–	–	–
Suricata suricatta	Suricate	2	1	4	7	3	6	2	3	6
Civettictis civetta	Civet	–	–	–	–	–	–	–	–	–
Genetta spp. mainly *G. genetta*	Small-spotted genet	1	4	3	2	4	2	2	1	7
Unspecified viverrids		–	–	1	1	1	–	–	–	–
Mellivora capensis	Honey badger	–	–	–	2	3	–	–	–	5
Ictonyx striatus	Striped polecate	4	3	4	2	4	2	–	–	1
Poecilogale albinucha	Striped weasel	–	–	–	–	–	–	–	–	–
Aonyx capensis or *Lutra maculicollis*	Otter	–	–	–	–	–	–	–	–	–
Felis lybica	African wildcat	–	2	2	3	–	1	–	–	1
Felis caracal	Caracal	–	–	1	2	–	3	–	–	–
Felis nigripes	Small-spotted cat	–	–	–	1	–	–	–	–	–
Unspecified felids		1	3	7	5	1	–	11	3	2
Canis spp. mainly *C. mesomelas*	Black-backed jackal	9	4	13	28	11	14	6	6	24
Otocyon megalotis	Bat-eared fox	21	21	20	18	7	19	16	12	10
Vulpes chama	Cape fox	1	–	1	–	–	–	1	1	2
Proteles cristatus	Aardwolf	4	3	–	1	2	2	–	–	1
Hyaena brunnea	Brown hyaena	–	–	–	–	1	–	–	–	–
Crocuta crocuta	Spotted hyaena	–	–	1	–	–	–	–	–	–
Xerus inauris	Ground squirrel	–	1	1	–	2	–	2	–	–
Paraxerus cepapi	Tree squirrel	1	–	–	–	–	–	–	–	–
Thryonomys swinderianus	Greater cane rat	–	1	–	1	–	–	–	–	–
Lepus spp., probably *L. saxatilis*	Scrub hare	–	–	–	–	–	–	–	–	–
Procavia capensis	Cape hyrax	–	–	1	–	1	–	–	1	–
Papio ursinus	Chacma baboon	–	–	–	–	–	–	–	–	–
Phacochoerus aethiopicus	Warthog	–	–	–	–	–	1	–	–	–
Sylvicapra grimmia	Duiker	–	1	1	–	1	1	–	–	–
Raphicerus campestris	Steenbok	–	–	–	1	1	–	–	–	–
Tragelaphus strepsiceros	Kudu	–	–	–	–	–	–	–	–	–
Taurotragus oryx	Eland	–	–	–	–	–	–	–	–	1
Damaliscus dorcas phillipsi	Blesbuck	–	–	–	–	–	–	–	–	–
Redunca arundinum	Reedbuck	–	–	–	–	–	–	–	–	–
Antidorcus marsupialis	Springbok	–	–	–	–	–	–	–	1	–
Equus burchelli	Zebra	–	–	–	–	–	–	1	–	1
Unspecified herbivores		–	–	–	–	–	–	3	3	–
Epomophorus wahlbergi	Wahlberg's epauletted fruit bat	–	–	–	–	–	–	1	–	–
Unspecified pteropodid, probably *E. wahlbergi*		–	–	–	–	–	–	–	–	–
Nycteris thebaica	Slit-faced bat	–	–	–	–	–	–	–	–	–
Unidentified chiropterid, possibly *Miniopterus schreibersii*		–	–	–	–	–	–	–	–	–
Unindentified chiropterid	Insectivorous bat	–	–	–	–	–	–	–	–	1
Other unspecified or unidentified animals*		–	1	–	–	–	–	–	–	–
Total wild animals		207	202	227	210	107	131	137	97	180
Total		475	397	455	638	406	395	565	568	741

* Probably includes domestic animals

Town) where the fox is the dominant host of rabies at present (OVI 1932–1992, unpublished records). During the evolution and spread of the outbreak lesser numbers of cases of the disease were recorded in the black-backed jackal, the aardwolf (*Proteles cristatus*), and on isolated occasions the Cape fox (*Vulpes chama*). Rabies has been diagnosed more frequently in antelope in the Cape Province than elsewhere in the country, particularly in small species such as the duiker (*Sylvicapra grimmia*), and this trend has been more marked since the increase in the incidence of the disease occurred in bat-eared foxes, jackals and aardwolves.

Veterinary officials in South Africa and Zimbabwe were conscious of the threat posed by the invasive canid form of rabies which had appeared in Namibia and Botswana at the end of the 1940s, and spread of the disease from Botswana into the northern Transvaal was duly recognized in June 1950, and thence into southern Zimbabwe by August, although subsequent investigations revealed that the virus had probably entered both countries some months earlier (De Kock 1949; Alexander 1952; Snyman 1953; Adamson 1954; Mansvelt 1956). The disease did not extend southwards in the relatively dry and sparsely inhabited north-western Transvaal, but spread to the more densely populated areas to the east and entered Mozambique in 1952 via the extreme north-eastern corner of South Africa, which at that time had not been incorporated into the Kruger National Park (Alexander 1952; Mansvelt 1956; Valadão 1968). Some 22 000 dogs were destroyed within two years in an attempt to control the disease in the northern Transvaal, and from 1952 onwards Flury LEP vaccine was used to immunize dogs in the area (Alexander 1952; Snyman 1953; Adamson 1954; Mansvelt 1956). The outbreak had subsided to a few sporadic cases by 1954, and although 181 414 dogs had been vaccinated by 1962, dog rabies has remained present in the independent and self-governing states in the north-eastern Transvaal (OVI 1932–1992, unpublished records; Mansvelt 1956; 1962).

Cases of rabies in black-backed jackals and cattle were recorded on bushveld ranches during the initial outbreak of the disease in the northern Transvaal in 1950, and over 3 000 jackals were poisoned from 1951–1956 with meat baits laced with strychnine in an attempt to control the disease (Mansvelt 1956). Attempts to control jackals were also made in Namibia, Botswana and Zimbabwe, and in the 1960s the explosive coyote-getter device was brought into use (Van Rensburg 1965; Foggin 1988). The campaigns generally provided only temporary and localized control of rabies, but by the mid 1960s the impression had been gained that the disease had not become permanently established in wild animals in the northern Transvaal (Mansvelt 1965). However, jackal and cattle rabies became a serious problem again in the mid 1970s, and it was thought that a further introduction of jackal rabies had occurred in the vicinity of Messina in 1974, from Zimbabwe across the Limpopo river (Brückner *et al.* 1978). Immunization of cattle with Flury HEP (high egg passage) vaccine was introduced in 1976 (Brückner *et al.* 1978), but the disease in jackals and cattle remains a problem in the ranching areas of the northern Transvaal. Attention has been drawn to the fact that where jackal rabies occurs in the northern Transvaal and Namibia, the number of cases of the disease recorded in domestic herbivores, particularly cattle, exceeds that in all vector species by up to three-fold or more, and that this ratio is reversed in areas where the yellow mongoose is the dominant vector (Barnard 1979a). Over the years, sporadic cases of rabies have also been recorded in civets (*Civettictis civetta*), honey badgers (*Mellivora capensis*), and antelope in the northern Transvaal, and isolated cases have been confirmed in genets, bat-eared foxes, hyraxes (*Procavia capensis*), the brown hyaena (*Hyaena brunnea*) and Selous' mongoose (*Paracynictis selousi*), which is nocturnal and solitary (OVI 1932–1992, unpublished records; Mansvelt 1956; Brückner *et al.* 1978). Furthermore, endemic rabies of the yellow mongoose extends to the Soutpansberg district in the northern Transvaal (OVI 1932–1992, unpublished records).

Rabies was thought to be endemic in central Mozambique from at least 1908 onwards, and was first confirmed in Tete district in 1950 (Valadão 1968). In 1952, the epidemic of dog rabies which was raging in the north-eastern Transvaal extended into Mozambique and spread rapidly throughout the central and southern districts of the country, where the disease has remained prevalent since that time (Valadão 1968). Rabies has been diagnosed predominantly in dogs in Mozambique and it is hyperendemic in the southernmost Maputo district where the population is densest, but monitoring and control of the disease has been hampered by prolonged civil war (Valadão 1968; Dias, Novoa & Cliff 1985; Lopes Pereira Pinto & Baulle 1988; Dias 1992). In 1954, dog rabies spread from Maputo district into Swaziland, where the occurrence of the disease was confirmed for the first time, and since then there have been periodic incursions of rabies from Mozambique into Swaziland and the adjoining portion of the Transvaal which lies between Swaziland and the southern boundary of the Kruger National Park (OVI 1932–1992, unpublished records; Hlatswako 1992).

In mid 1961, dog rabies spread from Maputo district in southern Mozambique into northern Natal in South Africa (districts which are currently administered separately as KwaZulu are considered to be part of Natal for purposes of the present discussion) (OVI 1932–1992, unpublished records; Mansvelt 1962; Maré 1962; Tarr, O'Grady & Jenkins 1962). The density

of the rural population in the coastal and many of the midlands districts of Natal favoured the spread of the disease in dogs, and the epidemic which followed the introduction of the virus into the province in 1961 was of an intensity unprecedented in South Africa. Vigorous efforts were made to control the disease (Mansvelt 1962), and the outbreak was finally brought to an end late in 1968 (OVI 1932–1992, unpublished records).

Rabies reappeared in the northern districts of Natal, adjacent to the Maputo district of Mozambique, in mid 1976 (OVI 1932–1992, unpublished records) at a time when there was an influx of refugees fleeing the unsettled conditions which followed the assumption of independence by Mozambique from Portugal. During the eight years since rabies had last been diagnosed the population of Natal had continued to burgeon, and since many rural inhabitants sought livelihoods in urban centres, informal settlements flourished, where uncontrolled dog populations provided fertile ground for epidemic spread of the disease. Dog rabies spread from Natal to the Transkei area of the eastern Cape Province in 1987, and by the early 1990s had reached the Ciskei area (OVI 1932–1992, unpublished records; Regional Veterinary Laboratory 1987–1992, unpublished records). Like Natal, the Transkei and Ciskei areas have dense rural and peri-urban populations, and the emergence of dog rabies in the east represents yet another development in the complex pattern of rabies in the Cape Province.

Since its re-introduction into Natal-KwaZulu in 1976, dog rabies has proved to be intractable. Approximately 75% of all cases of rabies recorded in dogs in South Africa since 1976 have occurred in Natal-KwaZulu, and dogs represent about 88% of all animals in which rabies has been recorded in the province during this period (OVI 1932–1992, unpublished records; Regional Veterinary Laboratory 1987–1992, unpublished records). Peak vaccination coverage of 59% of the estimated total dog population of Natal-KwaZulu was attained in 1980–1981 (Department of Agriculture 1940–1992, unpublished records; Swanepoel 1994) but the immunization of unrestricted dogs in informal settlements constitutes a formidable task which has been rendered increasingly difficult by the political unrest which has developed in the province. Consequently, inadequate vaccination coverage has been attained in recent years in the strategically important locations where the problem is most severe.

Prior to 1950, most cases of human rabies in South Africa resulted from bites by viverrids (and sporadically other animals) in the southern Transvaal, Orange Free State and Cape Province, but following the incursion of the canid virus into the northern Transvaal, and later Natal, dogs became the most important source of human infection. Currently, about 10–20 cases of human rabies are recorded each year in South Africa, mainly in association with dog bites in Natal-KwaZulu, but human disease is of growing importance in the eastern Cape Province (OVI 1932–1992, unpublished records; National Institute for Virology 1953–1992, unpublished records; Veterinary Laboratory, Transkei 1990–1992, unpublished records).

Monoclonal antibody studies have confirmed that virus strains associated with endemic viverrid rabies in Botswana and South Africa can be distinguished from the canid strain which appears to have spread through Namibia, Botswana, Zimbabwe and parts of South Africa from about 1947 onwards (National Institute for Virology 1953–1992, unpublished records; Schneider, Barnard & Schneider 1985; King 1991). Virus associated with the bat-eared fox in the northern and western Cape Province conforms to the canid type (National Institute for Virology 1953–1992, unpublished records; King 1991), and this tends to confirm the impression that apart from the putative spread of the canid virus across the northern Transvaal and through Mozambique into Natal, there may have been a further introduction of the virus into South Africa via the fox from Namibia.

The total range of species affected and numbers of cases of rabies which have been confirmed since regular monitoring was instituted in South Africa in 1928, up to 1992 inclusive, are summarised in Table 1, and annual figures are presented in Table 2. As far as possible, the information was derived from original laboratory records (OVI 1932–1992, unpublished records; National Institute for Virology 1953–1992, unpublished records; Regional Veterinary Laboratory 1987–1992, unpublished records; Veterinary Laboratory, Transkei 1990–1992, unpublished records). Original rabies records at the Veterinary Institute, Onderstepoort, remain available only for the years from 1967 onwards, but transcripts of the original records for the years 1932–1943, and 1952–1966 inclusive, had been prepared by one of the present authors (C.D.M.). Summarised figures could be derived for the years 1944–1951 from existing information (OVI 1932–1992, unpublished records; Department of Agriculture 1940–1992, unpublished records), although only combined totals could be determined for the two years 1944 and 1945 (Table 2). Neitz & Marais (1932), and Neitz & Thomas (1933; 1934) published detailed records for the years 1928–1933, but otherwise the information presented in Tables 1 and 2 cannot be derived accurately from publications or departmental reports: figures given for rabies cases recorded during particular periods are either impossible to relate to calendar years, or to reconcile with each other without overlaps or gaps, or else the publications and reports do not stipulate any or all species involved, or they deal with only a

particular region, or omit figures for the self-governing and independent states, or they present figures which are at a variance with laboratory records (Du Toit 1929; 1936; Snyman 1937; 1940; 1953; Alexander 1952; Henning 1956; Mansvelt 1956; Maré 1962; Tustin & Smit 1962; Lambrechts 1964; Neitz 1965; Zumpt 1969; Brückner *et al.* 1978; 1936; Barnard 1979a; b; Gummow 1985; Gummow & Turner 1986; Keightley, Struthers, Johnson & Barnard 1987; Swart 1989). It should be noted that Tables 1 and 2 include cases of infection with rabies-related viruses recorded in South Africa and Zimbabwe, as discussed below.

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Dog rabies spread from Natal into the north-eastern corner of Lesotho in 1982, when the disease was recorded there for the first time, and within two years it had spread throughout the country (Khomari 1988; Scott 1988; Khomari 1992). Rabies has been recorded in dogs, cats, cattle, sheep, goats, horses and donkeys in Lesotho (Table 1), but monitoring of the disease has proved to be difficult in the mountainous terrain of the country and human disease has been recorded with disproportionate frequency. There are few feral carnivores in the country and the disease has not been recorded in wild animals. Dog rabies reached the western border of Lesotho in the mid 1980s, but did not penetrate deeply into the Orange Free State where preventive vaccination had been undertaken, and where the dog population is less dense.

RABIES-RELATED VIRUSES

Large numbers of isolations of rabies virus (lyssavirus 1) were made from non-haematophagous bats in the Americas during the 1950s, and this prompted investigations elsewhere in the world. As a consequence, Lagos bat virus was isolated from straw-coloured fruit bats (*Eidolon helvum*) in Nigeria in 1956 (Boulger & Porterfield 1958), but it was not until 1970 that the virus was identified as a rhabdovirus antigenically related to, but distinct from, rabies virus (Shope, Murphy, Harrison, Causey, Kemp, Simpson & Moore 1970). In 1968, a virus was isolated from *Crocidura* sp. shrews trapped in Mokola Forest near Ibadan, Nigeria, and from a shrew found dead in Ibadan (Kemp, Causey, Moore, Odeola & Fabiyi 1972; Kemp, Ottis, Setzer & Moore 1974). Identification of the Mokola virus as a rhabdovirus related to rabies virus was reported in the same publication as the identification of Lagos bat virus, and hence the concept of a rabies-related subgroup of rhabdoviruses was established (Shope *et al.* 1970). In 1970, an adult male living in the Warmbaths district about 100 km north of Pretoria, South Africa, died of rabies-like disease five weeks after being bitten by an insectivorous bat, possibly *Miniopterus schreibersii* (Van der Merwe 1982), and a virus isolated from his brain was found to be yet another rabies-related virus; named Duvenhage after the victim (Meredith, Rossouw & Van Praag Koch 1971; Tignor, Murphy, Clarke, Shope, Madore, Bower, Buckley & Meredith 1977).

The three rabies-related viruses have been encountered in only a few countries of western and southern Africa where appropriate investigations have been undertaken (Table 3), and recently in Ethiopia (Mebatsion, Cox & Frost 1992). In general, isolates obtained from ostensibly healthy bats, shrews or rodents in surveys were deliberately subjected to tests appropriate for the identification of rabies-related viruses, whereas isolates obtained from specimens submitted from humans and lower animals for the investigation of suspected rabies, were only recognized as rabies-related viruses because the investigators concerned were alert to non- specific features which distinguished the infections from rabies: routine diagnostic procedures do not allow rabies and rabies-related viruses to be differentiated with certainty. Thus, the two isolations of Lagos bat virus made from cats in South Africa and Zimbabwe (Table 3), were both made from animals which had been vaccinated against rabies. The cases occurred in isolation from known cases of rabies, fluorescence was observed to be weak in diagnostic tests with polyclonal anti-rabies fluorescein conjugate, and the signs of disease manifested by the cat in Zimbabwe, lethargy and paresis without aggressiveness, were considered to be atypical of rabies (OVI 1932–1992, unpublished records; Foggin 1988; King & Crick 1988).

Isolations of Lagos bat virus from fruit bats in South Africa in 1980 (Table 3), were made from individuals observed to behave abnormally at a time when public awareness was heightened by the fact that dog rabies was in an epidemic phase in Natal (OVI 1932–1992, unpublished records). Fluorescence with polyconal anti-rabies conjugate was observed in the brains of 13 of the bats submitted from Natal (ten in 1980 and three in 1981), and all 13 cases are included in Tables 1 and 2. The affected individuals are believed to have been common epaulleted fruit bats (*Epomophorus wahlbergi*) although only one was positively identified. Only three of the brains from Pinetown and Durban which fluoresced in 1980 were cultured and, although two of the isolates obtained were at one stage reported to be Mokola virus (Foggin & Swanepoel 1985; Schneider *et al.* 1985), all three have been confirmed to be Lagos bat virus in monoclonal antibody tests (only these three positively identified isolates are included in Table 3) (OVI 1932–1992, unpublished records; National Institute for Virology 1953–1992, unpublished records; Meredith & Standing 1981; Crick, Tignor & Moreno 1982; King & Crick 1988). A further isolation of Lagos bat

TABLE 3 Total isolations of rabies–related viruses in Africa

Species	Isolations	Year	Country	Circumstances	References[c]
Lagos bat virus					
Eidolon helvum (fruit bat)	1	1956	Lagos, Nigeria	Survey	a, b
Micropterus pusillus (fruit bat)	1	1974	Bozo, Central African Republic	Survey	c, d
Epomophorus wahlbergi (fruit bat)	3[a]	1980	Pinetown/Durban, South Africa	Abnormal behaviour	e–h
Domestic cat	1	1982	Stanger, South Africa	Abnormal behaviour	f
Nycteris gambiensis (insectivorous bat)	1	1985	Kindia, Senegal	Survey	i
Eidolon helvum (fruit bat)	1	1985	Dakar, Senegal	Survey	i
Domestic cat	1	1986	Dorowa, Zimbabwe	Abnormal behaviour	f, j
Epomophorus wahlbergi (fruit bat)	1	1990	Durban, South Africa	Abnormal behaviour	k
Dog	1	1989–1990	Addis Ababa, Ethiopia	Abnormal behaviour	l
Mokola virus					
Crocidura sp. (shrew)	4	1968	Ibadan, Nigeria	Survey	b, m, n
Human	1	1969	Ibadan, Nigeria	Non-fatal encephalitis	o
Domestic cat	1	1970	Umhlanga Rocks, South Africa	Abnormal behaviour	h
Human	1	1971	Ibadan, Nigeria	Fatal encephalitis	p
Crocidura sp. (shrew)	1	1974	Yaounde, Cameroon	Survey	q
Dog	1	1981	Bulawayo, Zimbabwe	Abnormal behaviour	j, r–u
Domestic cat	6	1981–1982	Bulawayo, Zimbabwe	Abnormal behaviour	j, r–u
Lophuromys sikapusi (myomorph rodent)	1	1983	Botambi, Central African Republic	Survey	v
Domestic cat	1	1989–1990	Addis Ababa, Ethiopia	Abnormal behaviour	l
Duvenhage virus					
Human	1	1970	Warmbaths, South Africa	Fatal encephalitis	w, x
Miniopterus schreibersii (insectivorous bat)	1[b]	1981	Louis Trichardt, South Africa	Abnormal behaviour	h
Nycteris thebaica (insectivorous bat)	1	1986	Esigodini, Zimbabwe	Survey	j

[a] Only one bat positively identified as *E. wahlbergi*

[b] Identification of species based on circumstantial evidence

[c] References for Table 3

a Boulger & Porterfield 1958
b Shope *et al.* 1970
c Sureau, Germain, Herve, Geoffroy, Cornet, Heme & Robin 1977
d Sureau, Tignor & Smith 1980
e Crick *et al.* 1982
f King & Crick 1988
g Meredith & Standing 1982
h Schneider *et al.* 1985
i Anonymous 1985
j Foggin 1988
k Bishop & Swanepoel 1990
l Mebatsion *et al.* 1992
m Kemp *et al.* 1972
n Kemp *et al.* 1974
o Familusi & Moore 1972
p Familusi *et al.* 1972
q Le Gonidec, Rickenbach, Robin & Heme 1978
r Foggin 1982
s Foggin 1983
t Foggin 1985b
u Wiktor *et al.* 1984
v Saluzzo, Rollin, Daugard, Digoutte, Georges & Sureau 1984
w Meredith *et al.* 1971
x Tignor *et al.* 1977

virus was made from an *E. wahlbergi* bat found dead in Durban in 1990 (Tables 1, 2 and 3) (Bishop & Swanepoel 1990), a finding which suggests that the virus is endemic in Natal.

After 1968, Mokola virus was next isolated in 1969 from the cerebrospinal fluid of a young girl who suffered from non-fatal illness with fever and seizures, and in 1971 from the brain of a girl who died of paralytic disease, both in Ibadan, Nigeria (Familusi & Moore 1972; Familusi, Osunkoya, Moore, Kemp & Fabiyi 1972). The possibility that the rabies-related viruses were capable of spread among domestic carnivores was raised when Mokola virus was isolated from the brains of six cats and a vaccinated dog submitted from Bulawayo, Zimbabwe, in 1981 and 1982 for the investigation of suspected rabies (Table 3) (Foggin 1982; 1983; Wiktor, Macfarlan, Foggin & Koprowski 1984; Foggin 1985b; 1988). The findings in Zimbabwe prompted retrospective investigation of a virus which had been isolated in 1970 from a cat in Natal, South Africa, and which had been preserved because it reacted weakly in the original diagnostic immunofluorescence test with anti-rabies conjugate, and because no rabies had been recorded in the area for two years (Meredith 1970). The isolate was identified as Mokola virus (Table 3) (National Institute for Virology 1953–1992, unpublished records; Schneider *et al.* 1985; King 1991), but has also been reported as Lagos bat virus (Smith 1989).

Mokola virus has never been isolated from bats (Table 3), and in retrospect it is thought that the cat and dog infections observed in Zimbabwe in 1981 and 1982, were probably the result of spill-over from an epidemic in small mammals such as shrews or myomorph rodents (Foggin 1988). Although Mokola virus has not been isolated in southern Africa since 1982, antibody to the virus was found in rodents in Zimbabwe, particularly bushveld gerbils (*Tatera leucogaster*) (Foggin 1988), and it is notable that virus isolation and charaterization was not attempted on the brains of two greater canerats (*Thryonomys swinderianus*) from the northern Transvaal which fluoresced in diagnostic tests with anti-rabies conjugate in 1985 and 1987 (Tables 1 and 2) (Swart 1989).

Following its initial isolation from a human patient, Duvenhage virus was isolated in 1981 from a bat, possibly *M. schreibersii* (Van der Merwe 1982), caught in daylight by a cat in Louis Trichardt in the northern Transvaal (Schneider *et al.* 1985), and in 1986 from a common slit-faced bat (*Nycteris thebaica*) caught in a survey in south-eastern Zimbabwe (Table 3) (Foggin 1988). In 1963, prior to the recognition of the rabies-related viruses, a virus was isolated from an *N. thebaica* bat collected in a survey from a cave in the eastern Transvaal, but the isolate was simply described as rabies virus, presumably on the basis of histopathological lesions observed in mice, and is therefore included in Tables 1 and 2, but omitted from Table 3 (Mansvelt 1965). Furthermore, immunofluorescence with anti-rabies conjugate was observed in the brain of an unidentified insectivorous bat from the northern Transvaal in 1993, but no virus could be isolated for characterization with monoclonal antibodies, and consequently this diagnosis is also included in Tables 1 and 2, and omitted from Table 3.

Numerous viruses isolated in southern Africa from the brains of humans and lower animals which fluoresced in diagnostic tests with anti-rabies conjugate, have been screened with monoclonal antibodies, and, apart from the cases mentioned above (Table 3), no evidence of infection with rabies-related viruses has been found (National Institute for Virology 1953–1992, unpublished records; King 1991). The implication is that the rabies-related viruses have not adapted to spread in carnivores, but that sporadic infections may be encountered in humans and domestic animals, particularly cats (Table 3) which are predators of small mammals such as shrews, myomorph rodents and bats.

There have been numerous isolations of bat-associated lyssaviruses in Europe, and at first it was suspected that Duvenhage virus may have been introduced with bats from Africa, but it is now clear that there are two distinct subtypes, European bat lyssaviruses 1 and 2, associated with serotine and myotine bats respectively (King 1991).

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