

# Patterns of rabies cases in South Africa between 1993 and 2019, including the role of wildlife

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## ABSTRACT

Rabies is a global viral zoonosis endemic to South Africa, resulting in fatal encephalitis in warm-blooded animals, including humans. The loss of human lives and economic losses in rural areas through loss of livestock are substantial. A review was conducted of all confirmed animal rabies cases in South Africa from 1993 to 2019, with a total of 11 701 cases identified to species level to assess the role that wildlife plays in the epidemiology of rabies. A spatio-temporal cluster analysis using a discrete Poisson space-time probability model, accounting for underlying estimated dog and livestock densities, identified 13 significant clusters ( $p < .05$ ). These included four long-term clusters lasting more than 8 years in duration and seven short-term clusters lasting less than 2 years, with the remaining two clusters being of intermediate length. Outside of these endemic clusters, wildlife outbreaks in the remainder of South Africa were often less than one and a half years in duration most likely due to the rapid decline of wildlife vectors, especially jackals associated with rabies infection. Domestic dogs accounted for 59.8% of cases, with domestic cats (3.2%), livestock (21.1%) and wildlife (15.8%) making up the remainder of the cases. Yellow mongoose (*Cynictis penicillata*) was the most frequently affected wildlife species, followed by bat-eared fox (*Otocyon megalotis*), black-backed jackal (*Canis mesomelas*), meerkat (*Suricata suricatta*) and aardwolf (*Proteles cristatus*). Rabies in wildlife species followed different spatial distributions: black-backed jackal cases were more common in the north-western parts of South Africa, yellow mongoose cases more frequent in central South Africa, and bat-eared fox and aardwolf cases were more frequent in southern and western South Africa. Clusters often spanned several provinces,

showing the importance of coordinated rabies control campaigns across administrative boundaries, and high-risk areas were highlighted for rabies in South Africa.

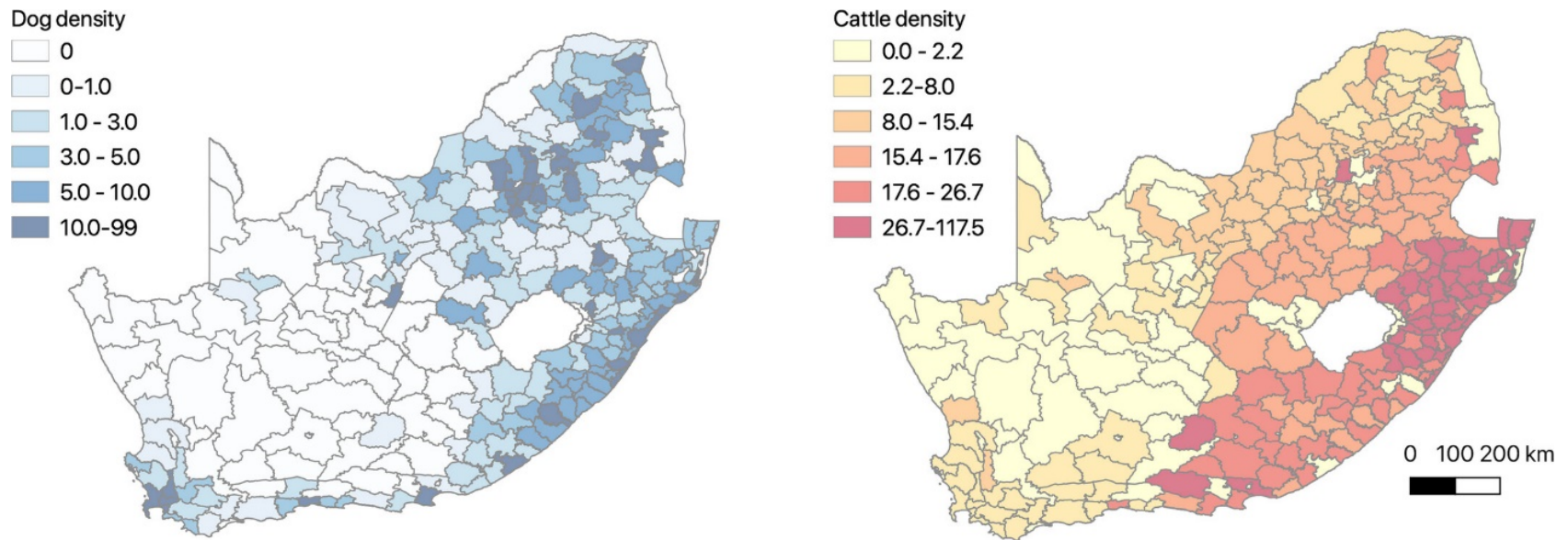
**KEYWORDS:** epidemiology, rabies, South Africa, spatio-temporal, wildlife, zoonosis

## 1 INTRODUCTION

Rabies is a viral disease caused by *Rabies lyssavirus* (RABV) belonging to the order Mononegavirales, family Rhabdoviridae, genus *Lyssavirus* (Amarasinghe et al., 2017). It is a negative-stranded RNA virus resulting in fatal encephalitis in domestic, wild animals and humans (Swanepoel et al., 1993). The number of human fatalities is thought to be under-reported in developing countries, where rabies is often endemic, and is suggested to amount to economic losses equivalent to \$4.7 billion worldwide (Hampson et al., 2015). In Africa, livestock losses are an important component of the cost of rabies (Knobel et al., 2005).

In South Africa, the control of rabies is difficult because of its endemic presence in domestic dogs in certain areas, as well as wildlife rabies in bat-eared fox (*Otocyon megalotis*), aardwolf (*Proteles cristatus*), yellow mongoose (*Cynictis penicillata*) and black-backed jackal (*Canis mesomelas*) (Swanepoel et al., 1993). Due to the variation in wildlife host ranges, rabies epidemiology often differs between the regions of South Africa. However, the domestic dog is still the most important species in the transmission of rabies, both in South Africa and the rest of the world (Morters et al., 2013; Sabetta et al., 2015). Dog rabies is endemic, especially in the densely populated rural areas of Limpopo (LP), Mpumalanga (MP) and KwaZulu-Natal (KZN) provinces of South Africa (Figure 1) (Zulu et al., 2009), and has persisted in KZN despite concerted efforts to control it by parenteral vaccination campaigns (Gummow et al., 2010). In 2011, 64% of dogs in KZN were reported to be vaccinated (Hergert et al., 2018), far higher than the 3.8% reported in 2004 (Gummow et al., 2010). The recommended minimum vaccination coverage is 70% for effective prevention of rabies outbreaks, but this was based on different environments and dog populations (Be-Nazir et al., 2018). Larger dog populations usually requiring higher vaccination coverage to prevent a major outbreak, although this could vary depending on the structure of the population (Coleman & Dye, 1996; Kaare et al., 2009). Failure of vaccination campaigns is thought to be due to the high density of dogs, especially in urban townships, and the high-population turnover, with most dogs being younger than 3 years of age (Hergert et al., 2018).

Opinions differ on the role of the black-backed jackal in the maintenance of rabies infection, with several authors suggesting that it has no maintenance potential due to the high number of jackal required for the spread of rabies and low aggression in undisturbed jackal populations (Cleaveland & Dye, 1995; McKenzie, 1993). However, jackals are thought to be maintenance hosts for rabies under enabling environmental conditions such as high density and increased population turnover with larger distances travelled by jackals (Bingham et al., 1999; Foggin, 1985). In Zimbabwe, both the side-striped jackal (*Canis adustus*) and the black-backed jackal are considered to be important in rabies transmission, with more cases occurring in the side-striped jackal (Bingham et al., 1999). Density of jackal populations may thus be a key factor in the maintenance and spread of rabies. Zulu et al. (2009) found that in the northeast of South Africa RABV (the LP-1 phylogenetic cluster) was only found in jackals and persisted over a 5-year period, so black-backed jackals maintained rabies infection independently from dogs.



**FIGURE 1.** Estimated density of dogs and cattle per km<sup>2</sup> in South Africa based on the 2011 human population census and gridded livestock of the world 2010 (Gilbert et al., 2010; Statistics South Africa, 2012). (The map was constructed using QGIS 3.4 using country and municipal boundaries)

RABV and its molecular epidemiology have been extensively studied in South Africa (Coetzee & Nel, 2007; Ngoepe et al., 2009; Zulu et al., 2009). These studies provided insight into the spread of rabies within the dog population and also its spread into wildlife species such as the black-backed jackal. From 1980 to 2005, wildlife accounted for just 5% of rabies cases diagnosed at the Onderstepoort Veterinary Institute (OVI) (Knobel et al., 2003; Sabeta et al., 2007). The first reported case of rabies in black-backed jackal was recorded in 1947, when rabies also started to appear in the bat-eared fox population in South Africa (Thomson & Meredith, 1993). Between 1952 and 1990, there was a median of 6.5 reported rabies cases in jackal per year (IQR: 6–7.25 cases/year) (Bishop, 1988; Thomson & Meredith, 1993). There have been a few descriptions of the occurrence and distribution of rabies in wildlife but they have mainly focused on the molecular structure of the different rabies isolates (Sabeta et al., 2011). Recently, the spill over of rabies from dogs to wildlife was investigated in the north-eastern part of South Africa, the Lowveld region (Grover et al., 2018) but there has been no analysis of spatio-temporal trends of rabies in the rest of South Africa to date.

To achieve the goal of the World Organisation for Animal Health (OIE) and the Global Alliance for Rabies Control of reducing human deaths due to dog-associated rabies to zero by 2030, it is essential to understand the spatial distribution and temporal patterns of rabies, as well as the hosts involved in the outbreaks in animals and the endemicity of rabies in any area (Rattanavipapong et al., 2019). In South Africa, rabies is a notifiable disease in humans and animals and surveillance is done at the national level by the National Institute for Communicable Disease (NICD) and the Department of Agriculture, Land Reform and Rural Development (DALRRD). All reports and samples from animals suspected of having contracted rabies are sent via the local State Veterinarian to the national rabies reference laboratory, where laboratory-confirmed cases are then recorded on the national database. The objective of this study was to provide a detailed description of the spatial distribution and temporal patterns of rabies from 1993 to 2019.

## 2 MATERIALS AND METHODS

A rabies case was defined as a laboratory-confirmed positive rabies result by direct fluorescent antibody test (Rupprecht et al., 2018). Data on animal rabies cases in South Africa from January 1993 to April 2019 were obtained from the national database maintained by DALRRD and were aggregated by month and local municipality (DALRRD, 2019). Rabies cases were assigned to the centroid of the local municipality. In 1993, the nine current provinces and municipalities were established for South Africa. The nine provinces (first-level administrative division) of South Africa are divided into district municipalities (second-level) and local municipalities (third-level). The 2011 census demarcation of local municipalities was used for case aggregation throughout, as there were only minor changes in local municipality boundaries over the 27-year study period (Statistics South Africa, 2012). Centroids were obtained using the polygon centroid plugin tool through QGIS (Version 3.4.9; QGIS Development Team, 2018). As there was a very low number of cases where species was not specified, they were excluded from the analysis ( $n = 14$ , 0.001%). Microsoft Excel version 16.45 was used for data management and descriptive statistics.

Spatio-temporal cluster analysis was done with SaTScan Version 9.6 (Kulldorff 2009), using a discrete Poisson space-time probability model on monthly aggregated data and scanning for clusters with high rates within a circular window (Kulldorff et al., 2005; Kulldorff & Nagarwalla, 1995). Clusters with  $p < .05$  were considered significant. The maximum temporal window was set as 120 months (10 years) as epidemics in South Africa occur every

8 to 10 years (Bishop et al., 2010). The maximum spatial cluster size was set as 287 km (The radius at which Ripley's reduced second moment function  $K(r)$  is maximized and where the point pattern becomes independent (Dixon, 2014)). The window with the highest log-likelihood ratio (LLR) was defined as the most important cluster, and all significant ( $p < .05$ ) clusters were shown. The  $p$ -value of the LLR was estimated through 999 Monte Carlo simulations (Kulldorff, 2001).

For cluster analysis, species were aggregated into companion animals (dog and cat), livestock (equine, bovine, ovine, caprine or porcine) and wildlife (all wildlife species) and used as covariate in the cluster analysis. For companion animal (dog and cat) populations at risk, dog density was used and calculated using the 2011 human census data for South Africa (Statistics South Africa, 2012), at a ratio of 13 humans to 1 dog for rural and of 21:1 for urban areas (Akerele, 2014; Conan et al., 2017; Evans et al., 2019; Hergert et al., 2018; Knobel et al., 2005; L  chenne et al., 2016). Gridded livestock of the world (GLW3) was used to aggregate livestock numbers (cattle, sheep, goats and horses) per local municipality (Gilbert et al., 2010). Land cover suitability was used to adjust population density, with mine building, urban residential, informal settlement and commercial industrial areas categorized as unsuitable (Department of Environmental Affairs, 2014). Population density per km<sup>2</sup> for dog and cattle are shown in Figure 1. Maps were generated using QGIS (Version 3.4.9) and RStudio (Version 1.0.153). A relative risk map was created by calculating the risk for a particular municipality for rabies during the entire time period, comparing case numbers to the population size at risk. It was calculated as the observed divided by the expected within the cluster divided by the observed divided by the expected outside the cluster.

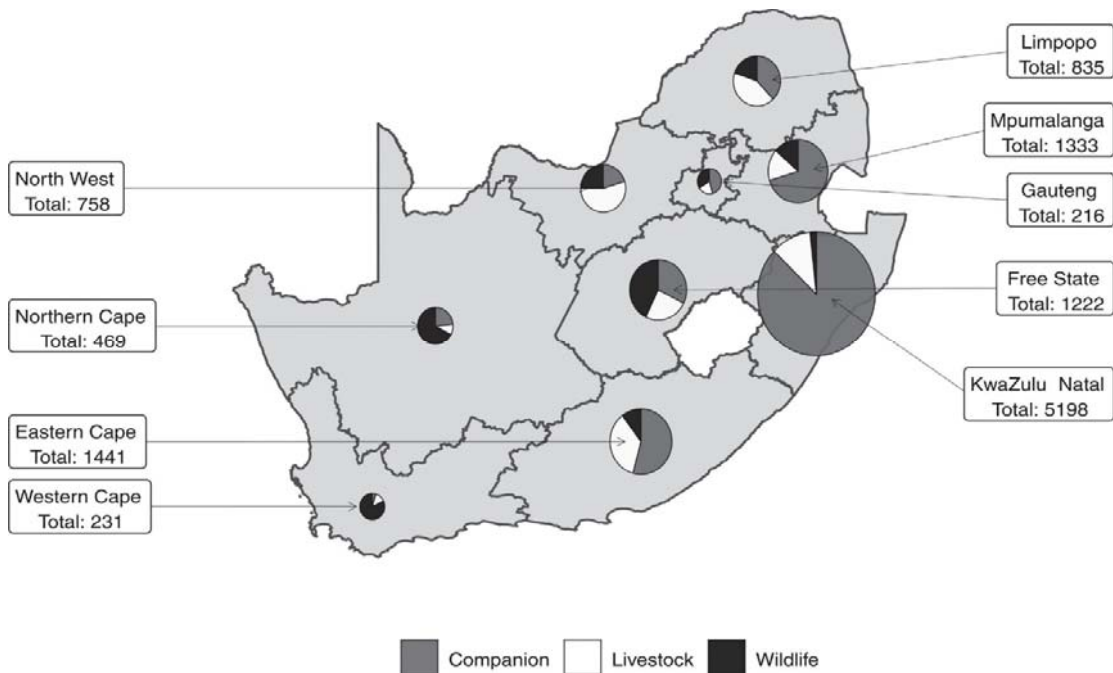
**TABLE 1.** Species associated with rabies in South Africa from 1993 to 2019, showing the percentage involvement of the species in overall rabies cases

Species	Scientific name	Cases	Percent
Domestic		9,853	84.21
Domestic dog	<i>Canis lupus familiaris</i>	7,001	59.83
Cattle	<i>Bos taurus</i>	1925	16.45
Domestic cat	<i>Felis catus</i>	379	3.24
Goat	<i>Capra hircus</i>	261	2.23
Sheep	<i>Ovis aries</i>	158	1.35
Horse	<i>Equus ferus caballus</i>	72	0.62
Farm animal	Species not identified	35	0.30
Pig	<i>Sus scrofa domesticus</i>	20	0.17
Avian	Species not identified	1	0.01
Ostrich	<i>Struthio camelus</i>	1	0.01
Wildlife		1848	15.79
Yellow mongoose	<i>Cynictis penicillata</i>	656	5.61
Bat-eared fox	<i>Otocyon megalotis</i>	378	3.23
Black-backed jackal	<i>Canis mesomelas</i>	287	2.45
Meerkat	<i>Suricata suricatta</i>	114	0.97
Aardwolf	<i>Proteles cristatus</i>	81	0.69
Slender mongoose	<i>Galerella sanguinea</i>	67	0.57
Marsh mongoose	<i>Atilax paludinosus</i>	31	0.26
Small-spotted genet	<i>Genetta genetta</i>	28	0.24
Large grey mongoose	<i>Herpestes ichneumon</i>	24	0.21
Cape fox	<i>Vulpes chama</i>	21	0.18
Cape ground squirrel	<i>Xerus inauris</i>	16	0.14
African wildcat	<i>Felis lybica</i>	16	0.14
Side-striped jackal	<i>Canis adustus</i>	14	0.12
Honey badger	<i>Mellivora capensis</i>	13	0.11
Striped polecat	<i>Ictonyx striatus</i>	13	0.11
Common duiker	<i>Sylvicapra grimmia</i>	10	0.09
White-tailed mongoose	<i>Ichneumia albicauda</i>	9	0.08
Caracal	<i>Caracal caracal</i>	8	0.07
African civet	<i>Civettictis civetta</i>	7	0.06
Kudu	<i>Tragelaphus strepsiceros</i>	7	0.06
Rock dassie	<i>Procavia capensis</i>	6	0.05
Wild dog	<i>Lycaon pictus</i>	5	0.04
Small-spotted cat	<i>Felis nigripes</i>	4	0.03
Spotted hyaena	<i>Crocota crocuta</i>	4	0.03
Serval	<i>Leptailurus serval</i>	4	0.03
Eland	<i>Taurotragus oryx</i>	3	0.03
Viverridae	Species not identified	3	0.03
Banded mongoose	<i>Mungos mungo</i>	2	0.02
Burchell's zebra	<i>Equus quagga burchellii</i>	2	0.02
Lion	<i>Panthera leo</i>	2	0.02
Selous' mongoose	<i>Paracynictis selous</i>	2	0.02
Steenbok	<i>Raphicerus campestris</i>	2	0.02
Cape clawless otter	<i>Aonyx capensis</i>	2	0.02
Large spotted genet	<i>Genetta tigrina</i>	1	0.01
Cape buffalo	<i>Syncerus caffer</i>	1	0.01
Blue wildebeest	<i>Connochaetes taurinus</i>	1	0.01
Brown hyaena	<i>Hyaena brunnea</i>	1	0.01
Chacma baboon	<i>Papio ursinus</i>	1	0.01
Dwarf mongoose	<i>Helogale parvula</i>	1	0.01
Rodentia	Species not identified	1	0.01

### 3 RESULTS

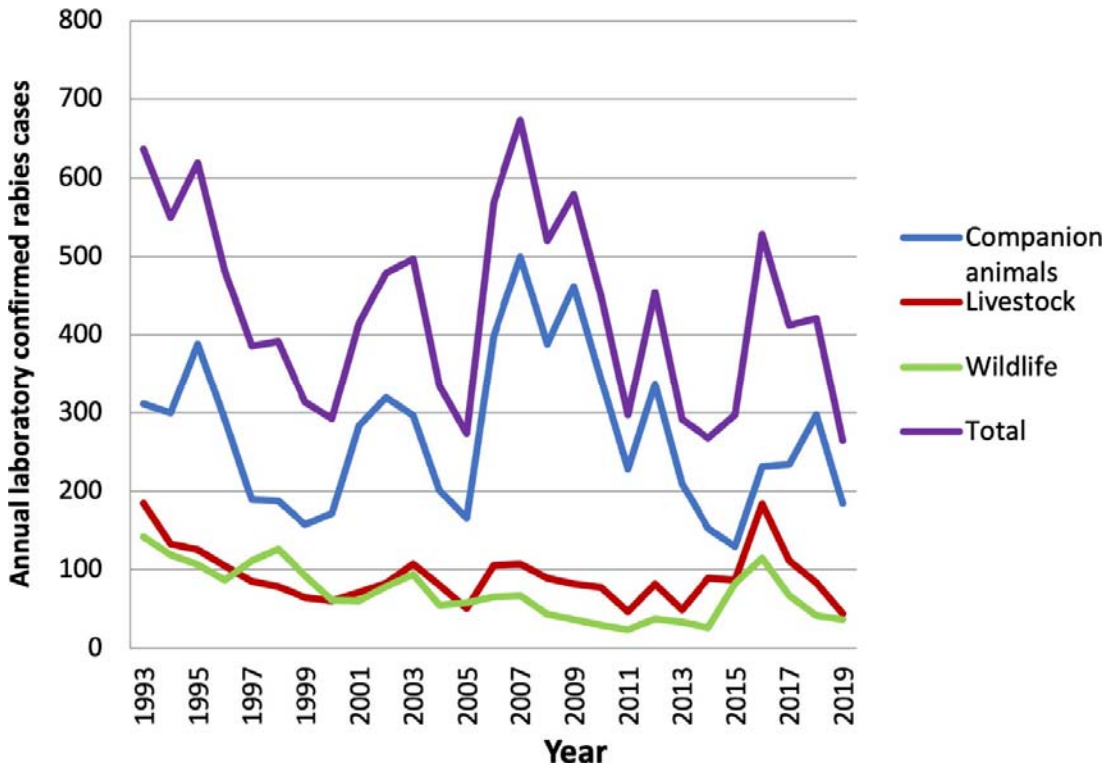
There were a total of 11 732 laboratory-confirmed animal rabies cases between January 1993 and April 2019 in South Africa, of which 11 701 cases were included in the SatScan analysis, since 31 records (0.3%) lacked location or species data (Table 1). The median annual number of confirmed animal rabies cases was 436 (range: 264–673; IQR: 318–526). Dogs constituted the majority of cases (59.8%) and domestic cats were responsible for 3.2% of cases. In livestock, cattle were the most frequent with 15.8% of total cases, followed by goats (2.1%), sheep (1.3%) and equines (0.6%). Wildlife was responsible for 15.8% of all animal cases. Yellow mongoose was the most frequently affected with 35.5% of wildlife cases, followed by bat-eared fox (20.5%) and black-backed jackal (15.5%). Aardwolf represented 4.4% of wildlife cases and other mongoose species (7.4%) were sporadically reported (Table 1).

The densely populated province of KZN (Figure 1) in the east of South Africa had the highest number of rabies cases by province, with 44% of the total cases from 1993 to 2019, followed by the Eastern Cape and MP. Wildlife cases were highest in the Free State (central South Africa), followed by the Northern Cape (Figure 2). Two cases have been found in avian species in this study (<0.02%).



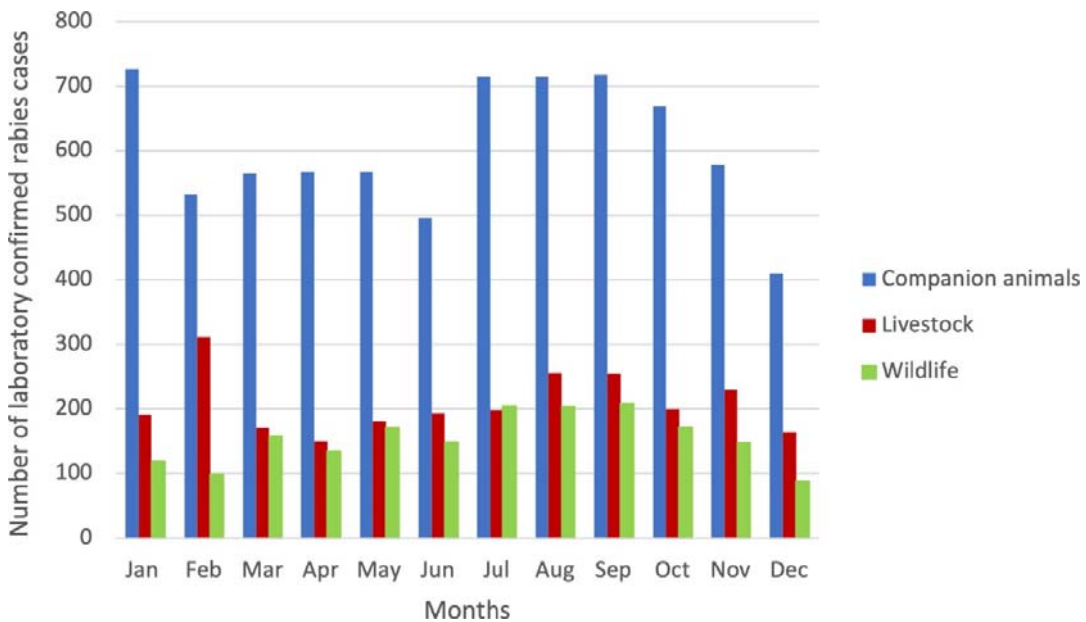
**FIGURE 2.** Map of rabies cases in South Africa 1993–2019 showing species categories involved by province. The diameter of the pie chart is proportional to the number of reported cases. (The map was constructed using RStudio version 1.0.153 using provincial boundaries)

The number of laboratory-confirmed cases of rabies in companion animals in South Africa between 1993 and 2019 peaked in 2007 with 499 cases reported (Figure 3). Companion animals showed a median of 283 cases per annum (IQR: 188–328), followed by 83 livestock cases per annum (IQR: 74–106) and 65 wildlife cases per annum (IQR: 39–93).



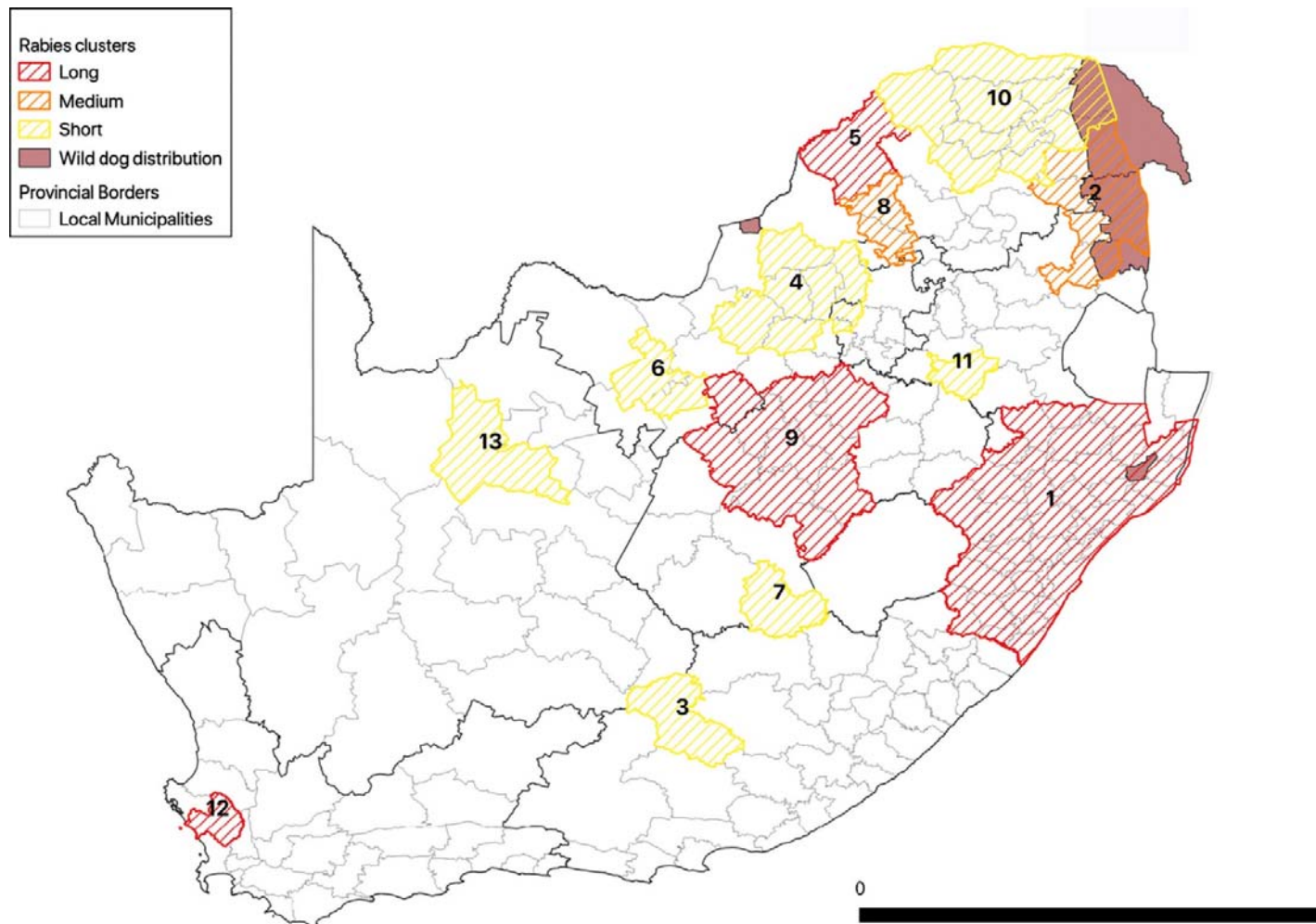
**FIGURE 3.** Annual confirmed rabies cases in companion animals, livestock and wildlife in South Africa from 1993 to 2019

Monthly cumulative rabies cases for domestic animals over the entire study period showed no strong seasonal patterns (Figure 4), although companion animal cases increased in January and from July to October.



**FIGURE 4.** Monthly cumulative number of confirmed cases of rabies in companion animals, livestock and wildlife in South Africa from 1993 to 2019





**FIGURE 5.** Spatio-temporal cluster analysis of rabies outbreaks in South Africa from 1993 to 2019 showing 13 significant clusters. The temporal length of the clusters is indicated by colour: yellow (short), orange (medium) and red (long). For details of each cluster refer to Table 2. (The map was constructed using QGIS 3.4 using country and municipal boundaries and wild dog distribution with permission from IUCN red data list <https://www.iucnredlist.org> (Woodroffe & Sillero-Zubiri, 2012))

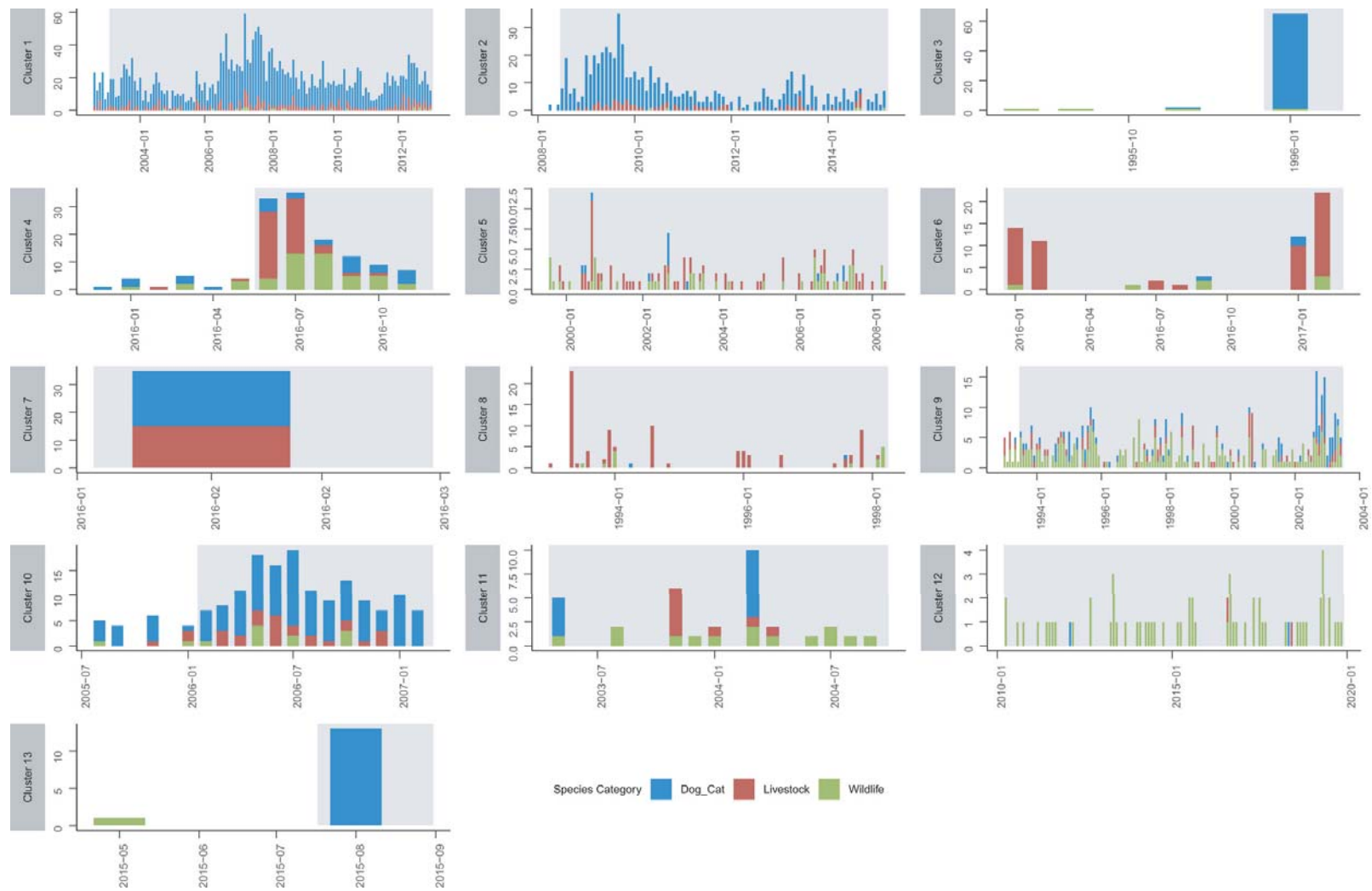
## Spatio-temporal cluster analysis

Analysis for spatio-temporal clusters of rabies cases in South Africa from 1993 to 2019 revealed 13 significant clusters, varying considerably in duration from 1 month to 10 years (Table 2). There were four long-term clusters (Clusters 1, 5, 9, 12) lasting more than 8 years, seven short term clusters lasting less than 1.5 years and two intermediate clusters (2, 8) lasting 4 and 8 years (Figure 5).

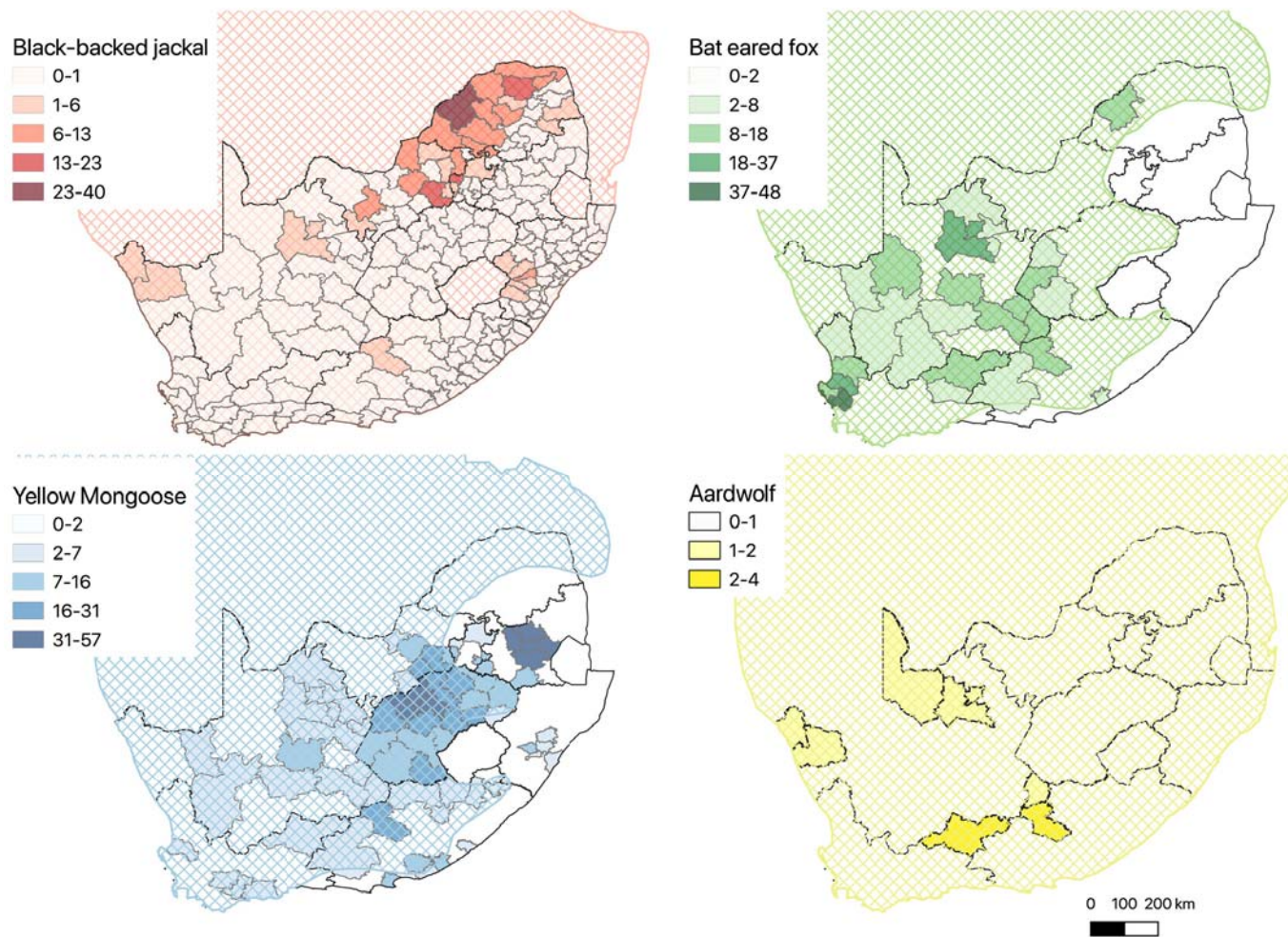
**TABLE 2.** Significant spatio-temporal clusters of rabies cases identified in South Africa, from 1993–2019

Cluster	Start date	End date	Cluster duration (years)	No. of districts	Provinces	Log-likelihood ratio ( <i>p</i> -value)	Observed cases	Expected cases
1	2003–02–01	2013–01–31	10	48	KZN	1522 ( <i>p</i> < .001)	2,353	628.1
2	2008–07–01	2015–03–31	6.75	5	LP, MP	776.3 ( <i>p</i> < .001)	624	76.4
3	1996–01–01	1996–01–31	0.08	1	EC	312.2 ( <i>p</i> < .001)	65	0.2
4	2016–06–01	2016–11–30	0.5	8	NW, GP	198.8 ( <i>p</i> < .001))	114	7.9
5	1999–08–01	2008–05–31	8.83 s	1	LP	173.6 ( <i>p</i> < .001)	142	17.5
6	2016–01–01	2017–02–28	1.16	2	NW	158.3 ( <i>p</i> < .001)	66	2.3
7	2016–02–01	2016–02–29	0.08	1	FS	157.5 ( <i>p</i> < .001)	35	0.1
8	1993–05–01	1998–03–31	4.91	2	LP	149.6 ( <i>p</i> < .001)	95	7.9
9	1993–07–01	2003–06–30	10	9	FS, NW	133.8 ( <i>p</i> < .001)	410	163.1
10	2006–02–01	2007–02–28	1.07	11	LP	131.9 ( <i>p</i> < .001)	145	25.75
11	2003–05–01	2004–09–30	1.42	1	MP	61.5 ( <i>p</i> < .001)	33	2.0
12	2010–04–01	2019–11–30	9.66	1	WC	57.1 ( <i>p</i> < .001)	65	12.0
13	2015–08–01	2015–08–31	0.08	1	NC	42.8 ( <i>p</i> < .001)	13	0.2

Clusters 1 and 2 were long and medium length clusters associated with dogs (Figures 5 and 6). Cluster 3 seemed to have started in domestic dogs and then became established in wildlife, marsh mongoose (*Atilax paludinosus*). There were dog and jackal cases prior to the start of cluster 4 but for the next 6 months, it mainly contained wildlife (black-backed jackal) and livestock cases. Cluster 5 seemed to display an endemic pattern associated with wildlife rabies - black-backed jackal and bat-eared foxes in particular - only occasionally involving domestic dogs. Cluster 6 was associated with cases mainly in black-backed jackal and livestock, with only a few domestic dog cases. Cluster 7 was a domestic dog cluster which spread to livestock. Cluster 8 was a medium length wildlife cluster associated with yellow mongoose and occasionally involving other wildlife species and domestic dogs. Clusters 9, 11 & 12 displayed a low grade, long-term infection in wildlife, involving mainly yellow mongoose in clusters 9 & 11, and mainly bat-eared foxes in cluster 12. Cluster 10 was centred around domestic dogs but involved some black-backed jackals (*n* = 9) and livestock.



**FIGURE 6.** Analysis of rabies clusters in South Africa by species composition from 1993 to 2019. Clusters are shown in grey and any cases within six months prior to cluster in the same geographic area are also shown



**FIGURE 7.** Distribution of number of rabies cases reported in wildlife in South Africa, 1993–2019, by local municipality showing the species distribution in chequered colour (Do Linh San et al., 2015; Green, 2015; Hoffmann, 2014a, 2014b) (The map was constructed using QGIS 3.4 using country and provincial boundaries and species distribution with permission from IUCN red data list <https://www.iucnredlist.org>)

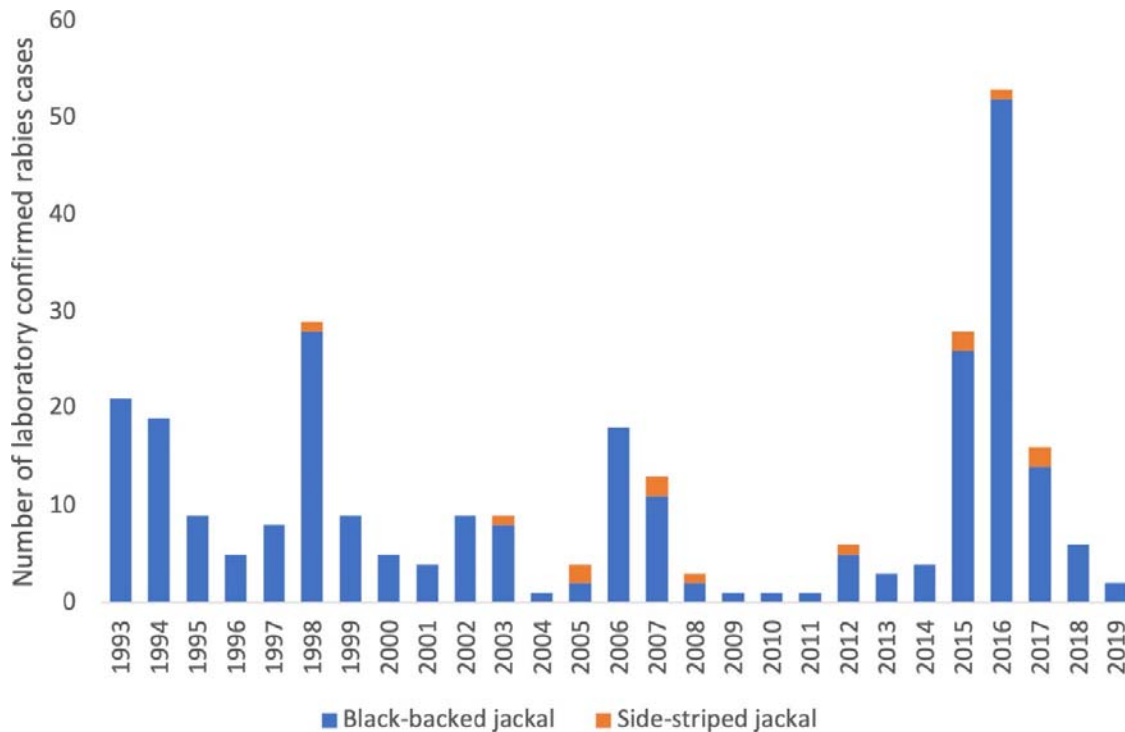
Cluster 13 was a short domestic dog outbreak of unknown origin as three months prior a common duiker was found positive, but no other wild carnivores were involved.

### Wildlife rabies

Wildlife species were reported in 9 out of 13 clusters. Yellow mongoose rabies case numbers have decreased since 1993 with the lowest reported annual incidence ( $n = 3$ ) in 2011 and 2014 and a slight increase in 2015 but staying with a median of 17 cases per annum (IQR: 7.5–38.5) over the entire period of analysis. Bat-eared fox case numbers were relatively stable with a median of 14 cases per annum (IQR: 10–17.5). Black-backed jackal had a median of 7 rabies cases per annum (IQR: 3.5–14.5) with the highest number ( $n = 53$ ) reported during the 2016 outbreak (cluster 4). Other wildlife species combined had a median of 20.5 cases per annum (IQR :13.5–25).

Black-backed jackal cases were seen in north-western region of South Africa (Figure 7). Bat-eared fox cases were important in the western half of South Africa. Yellow mongoose cases were common in the central part of South Africa. Some rabies cases in yellow mongoose were distributed outside the distribution for the species and might have been misidentified. Aardwolf rabies cases were seen in less populated areas of western South Africa (Figure 7).

Jackals were responsible for 15.5% of rabies cases in wildlife and constituted 2.6% of all rabies cases over the entire study period, varying between 0.2% and 10.0% per annum. The number of rabies cases in jackal appeared to show a cyclical pattern in South Africa, with an increase in reported cases approximately every 3 to 8 years (Figure 8).

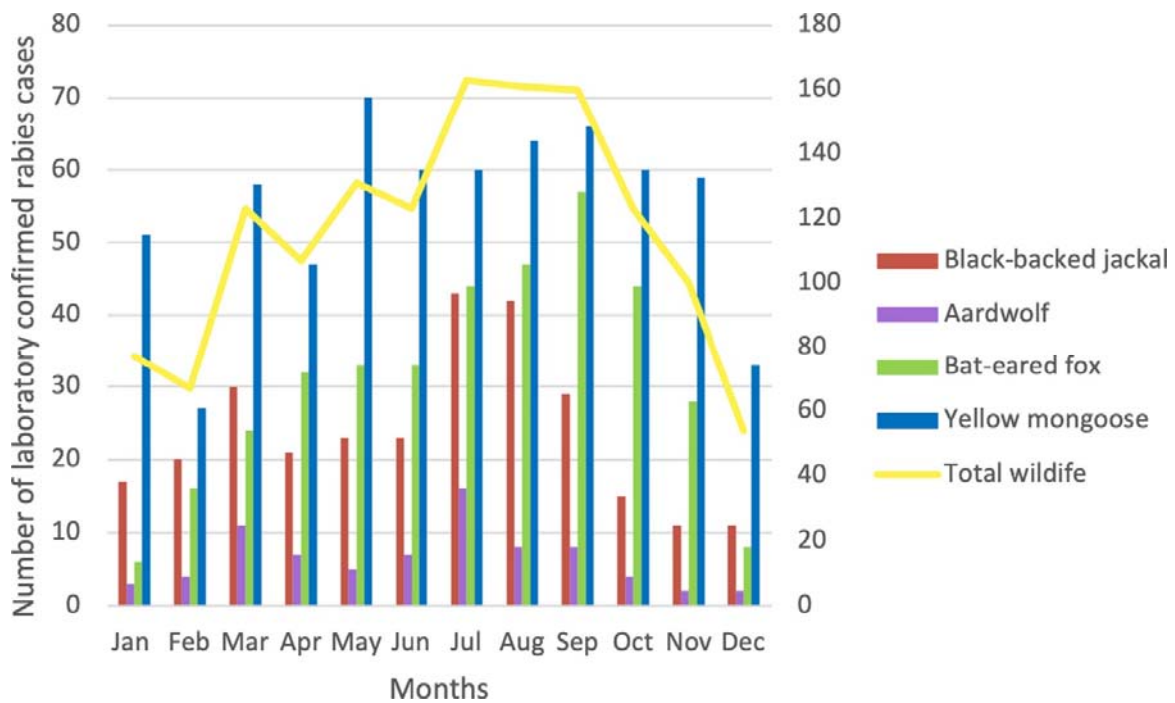


**FIGURE 8.** Number of rabies cases reported per year in jackals in South Africa from 1993 to 2019

In this study, the black-backed jackal was responsible for 92% of reported rabies cases in jackals from 1993 to 2019. There were 274 reported rabies cases in black-backed jackal in

South Africa from January 1993 to December 2019, and 13 cases in side-striped jackal: however, some ( $n = 6$ ) of the latter occurred outside their distribution area and were therefore likely misidentified black-backed jackals.

Monthly analysis of cumulative rabies cases showed two peaks in cases of rabies in black-backed jackals, with the main peak in July-August and a smaller peak in March. Aardwolf case numbers peaked in July. Bat-eared fox rabies cases showed the highest peak in July to October. Yellow mongoose case numbers were highest from May to November (Figure 9).

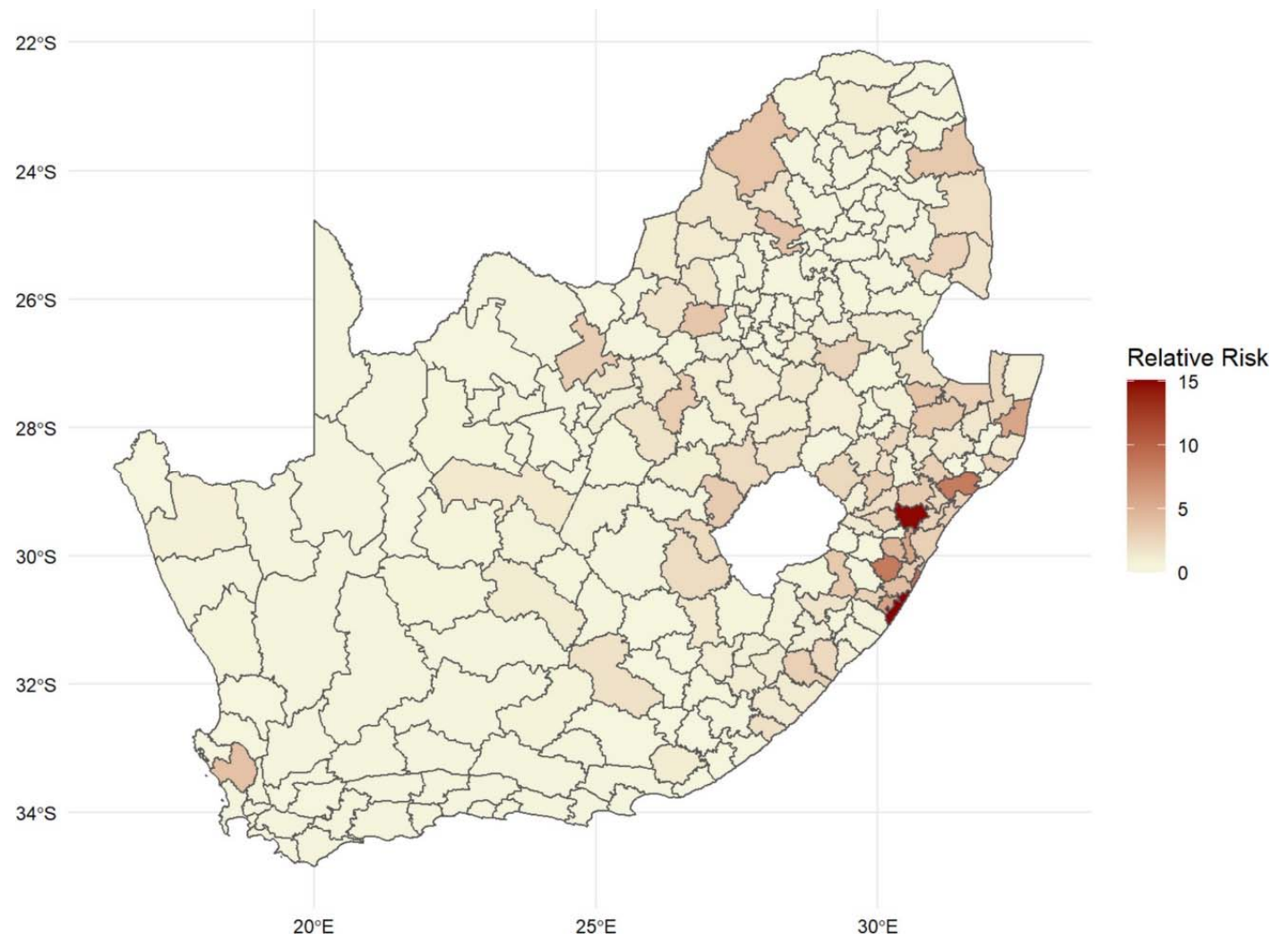


**FIGURE 9.** Number of confirmed cases of rabies in black-backed jackal, aardwolf, bat-eared fox and yellow mongoose in South Africa from 1993 to 2019, by month. Total wildlife case numbers are shown in right axis

A relative risk map of rabies cases in South Africa showed that certain municipalities of False Bay, Uthungulu, uMashwathi, uMlalazi and Hibiscus Coast in KZN have significantly higher risk of disease (Figure 10).

#### 4 DISCUSSION

Rabies eradication remains a challenge in South Africa, due at least partly to its presence in both domestic dog and wildlife populations, and the spatio-temporal analysis shows that wildlife has been involved in the majority of observed clusters between 1993 and 2019. The failure of rabies control is thought to be more likely due to economic and logistical constraints (Perry, 1993). Mollentze et al. (2014) suggested that identification of core rabies clusters in endemic areas and targeted vaccination campaigns would allow control of rabies over larger areas. The spatio-temporal cluster analysis in this study highlights several areas where rabies is endemic across an extended area. Long-term cycles in dogs are seen in the coastal region in the south-eastern part (KZN) and in the eastern part of South Africa. These long-term clusters should be addressed with continued vaccination in the area, especially where there is a high canine density and turnover of dogs. Cluster 1, which was an endemic cluster in domestic dogs in KZN identified in this study since 2003, ended after 10 years due



**FIGURE 10.** Relative risk map of rabies in domestic and wild animals for South Africa estimated from the 1993 to 2019 reported rabies cases (The map was constructed using RStudio version 1.0.153 using provincial boundaries)

to massive dog vaccination campaign together with public education and awareness, showing the positive effects of a one-health approach on rabies cases. The campaign ended in 2014 and cases in KZN have been steadily rising although not yet established as a new cluster (LeRoux et al., 2018). The KZN province continues to have the highest number of rabies cases in South Africa, which poses a risk not only to the local human population but is also a threat to the rest of South Africa. The rabies outbreak in southern Johannesburg in 2011 was traced back to an infected dog from an endemically infected area in KZN (Sabeta et al., 2013).

The significance of wildlife in rabies transmission in South Africa is emphasized when taking into account population densities of domestic animals and livestock in identifying clusters of rabies. Wildlife played an important role in the epidemiology of rabies in nine out of the 13 clusters identified either by being the likely index cases or maintaining the cluster. After yellow mongoose, black-backed jackal and bat-eared fox are the other two most important wildlife hosts in South Africa. Wildlife rabies cases occurred throughout South Africa, but wildlife cases depend on species distribution and density of wildlife in the area. In jackals, disturbance in the population, e.g. due to culling has been associated with an increased risk of rabies, while protected areas generally do not support rabies in jackal in South Africa (Bingham et al., 1999; McKenzie, 1993). Higher densities of black-backed jackal are found in the northern parts of South Africa in a variety of biomes but usually in the drier areas with rainfall below 1,000 mm annually (Skinner & Chimimba, 2005b). Jackals accounted for 15.5% of wildlife rabies in this study, which is a large apparent increase from the 5% of wildlife cases reported between 1928 and 1992, despite wildlife cases overall having decreased from 41% of all between 1928 and 1992 (Swanepoel et al., 1993) to 15.8% between 1993 and 2019.

However, the 15.5% of wildlife rabies cases in jackals in this study (3.2% of total rabies cases) is still below the 25% of confirmed total rabies cases that were attributed to side-striped and black-backed jackals in Zimbabwe (Bingham & Foggin, 1993). Difference between Zimbabwe and South Africa might be due to the fact that only black-backed jackals are involved in rabies epidemics in South Africa and cases in black-backed jackals are similar between the two countries in seasonal occurrence. Outbreaks of rabies in jackals in Zimbabwe have been linked to commercial farming practices in that country that favour rabies outbreaks, such as abundant food resources, high population turnover and lack of apex predators (Bingham, 2005; Swanepoel, 2004). Jackals are tolerated on commercial farms in Zimbabwe and there is suitable environment for breeding that allows jackal numbers to increase in those areas above the threshold of 1 jackal/km<sup>2</sup> that supports rabies outbreaks (Rhodes et al., 1998).

The 2016 rabies outbreak in the North West (NW) and Gauteng (GT) (cluster 4) was most likely initiated by dogs, indicated by cases prior to the start of the cluster, but once it was introduced into the susceptible jackal population it spread through the naïve population. The population of jackal in the area prior to the rabies outbreak was estimated at 0.64 jackal/km<sup>2</sup>, but the outbreak resulted in a 80%–93% reduction in a monitored jackal population in the north-western parts of Gauteng (Snyman, 2020), similar to losses seen in other naïve African carnivore populations (Randall et al., 2006). Domestic dogs are often implicated in the introduction of rabies to wildlife (Hampson et al., 2007). The periodicity of rabies outbreaks in jackals in South Africa between 1993 and 2019 (every 3 to 8 years) is similar to those in Zimbabwe where they occur every 4 to 8 years (Bingham & Foggin, 1993). Outbreaks appear to have increased in frequency in South Africa, with outbreaks occurring 3 years after a



previous one, an increase from the 5-year interval reported prior to 1993 (Brückner, 1993). This could reflect an increase in rate of contact between domestic dogs and jackals, particularly at the margins of rapidly expanding peri-urban areas. Particular attention should be paid to vaccination of dogs in such areas. In Zimbabwe up to half of rabies cases in dogs are associated with infection from jackals (Bingham et al., 1999a).

Rabies in wildlife seems to peak from May to November, the dry winter months, concomitant with a shortage of resources in most areas. Jackals and likely also other wild species, will increase their home ranges in response to reduced food availability (Ferguson et al., 1983). In jackals specifically, rabies cases peaked in July and August, corresponding with the jackal's mating season, with a secondary peak in March associated with the dispersal of the young (Rowe-Rowe, 1975; Skinner & Chimimba, 2005b). The increased number of jackal and increased contact rates between individuals likely facilitate the spread of rabies. The same pattern is seen in aardwolf, with a peak in July, corresponding to their short mating season in South Africa from the end of June to middle of July (Skinner & Chimimba, 2005a). Bat-eared foxes showed the highest peak in cases during July to October in this study. Bat-eared foxes forage in groups but groups split up prior to mating at the end of July and travel over greater areas, which can contribute to the spread of rabies (Nel, 1993). Food patches such as termites are shared between several family groups, which will further facilitate the spread of rabies (Nel, 1993). Rabies outbreaks in bat-eared foxes in the Serengeti were of short duration (Maas, 1993), which contrasts to this study where rabies persisted in the bat-eared fox population over several years as seen in clusters 5 and 12. Yellow mongoose cases peaked during the second half of the year, which may correspond to an increase in births and eviction of subadults from burrows due to food shortages (Taylor, 1993). Bovine cases peaked in February towards the end of summer (hot, wet season), which might be at least partly attributable to the increase in rabies in mongooses in January then spreading to livestock, such as was seen in clusters 8, 9 and 10. This was also seen in Namibia, where rabies cases are more frequent during the rainy season (January to June) in both wildlife and domestic animals (Hikufe et al., 2019).

Rabies virus transmission cycles are considered to be independent of each other in different wild canid and mongoose species (Sabeta et al., 2015), which is supported by the cluster analyses in this study, with only one of the clusters (Cluster 5) involving two wild canid species (black-backed jackal and bat-eared fox). The mongoose rabies virus biotype usually results in a dead end infection in other canids (Van Zyl et al., 2010).

Although this is a large data set over a long-time period, there might still be reporting bias, which potential could have influenced some of the findings. Rabies in wildlife is likely to be significantly under-reported since not all wild animals that die are evaluated for rabies, and during outbreaks not all cases of both domestic animals and wildlife are sent to a laboratory for diagnostic confirmation. The land use of an area might also have affected the reporting of rabies cases in wildlife with cases in communal farming areas potentially being under-reported as there might be no transport available to the local state veterinary services (Hikufe et al., 2019). In Namibia, the number of reports of rabies cases decreased both in domestic animals and wildlife the further they were from the state laboratory (Hikufe et al., 2019), while higher poverty in an area was directly related to reduced surveillance in Latin America (Arias-Orozco et al., 2018). So, there is a high likelihood that rural areas with high poverty did not report as accurately as more affluent areas. Public awareness in KZN has increased since 2014 due to targeted campaigns, which would have also improved reporting in the

province. The combination of disease data with environmental surveillance can assist in guiding future interventions for South Africa making control strategies more effective.

## 5 CONCLUSION

Rabies control remains a challenge in South Africa due to the long-term persistence of endemically infected areas with high dog densities and low vaccination coverage, as well as the persistence of rabies in wildlife and the potential of wildlife species to perpetuate outbreaks. This is exacerbated by changes in land use and farming practices, as well as increases in human and dog populations. The location and duration of rabies clusters provide an indication of areas with high rabies occurrence and persistence in both dogs and wildlife. This could be used to identify and target areas of high risk with parenteral and/or oral vaccination of domestic animals and wildlife, as well as other risk mitigation measures.

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. This study was approved by the University of Pretoria Ethics Committee (V149-16) and the Department of Agriculture, Land Reform and Rural Development (12/11/1/8).

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## CONFLICT OF INTEREST

None.

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