BMC Veterinary Research

RESEARCH

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Epidemiology of wild animal rabies in Namibia from 2001 to 2019: implications for controlling the infection in domestic animals

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Abstract

Background Rabies is an acute, fatal zoonosis of mammals that is endemic in Namibia. Wild animals have been implicated as reservoirs of the infection around the world. In this retrospective study, passive surveillance data (2001–2019) for wild animal rabies in Namibia were retrieved from the Directorate of Veterinary Services and analysed. The number, spatiotemporal epidemiology, and clinical presentation of rabies cases were assessed and compared among animal species, land use systems and regions.

Results The overall positive rate was 64.8% (1059/1635). Rabies infected 33 out of 52 wild animal species tested. The majority of cases were in Greater Kudu (*Tragelaphus strepsiceros*) (71.3%, $n=755/1059$), followed by the black-backed jackal (*Canis mesomelas*) (17.1%, 181/1059), eland (*Taurotragus oryx*) (5.1%, 54/1059), and 30 other wild animal species with low infection rates. Most positive cases (72.8%, 771/1059), and infected wild animal species ($n=26$) were from commercial farms. Rabies cases were clustered in the central-western regions of the country (Otjozondjupa, $n=373$; Khomas, $n=210$; Erongo, $n=123$; Omaheke, $n=105$; and Kunene, $n=154$). Local Moran analysis revealed that the Otjozondjupa region was a significant high-risk cluster of rabies ($p=0.0096$). The global Moran's I analysis by Monte Carlo permutations confirmed significant positive spatial autocorrelation of overall rabies cases from wild animal species in Namibia (Moran's $I=0.13$; $p=0.042$). Rabid animals presented the typical clinical signs of rabies. Jackals were responsible for most human and domestic animal bites (80%, 76/95). The number of rabies cases fluctuated over the years, but a clear decline was apparent from 2014 to 2019. The aggregated rabies cases were higher from January to June and lower from July to December.

Conclusions The results of this study confirm that rabies affects various wild animal species in Namibia, which may act as reservoirs of infection and hinder the control and elimination of dog-mediated rabies. A multi-sector One Health approach towards rabies control anchored on pet vaccination is recommended at Namibia's human-wildlife-livestock interfaces. Innovative strategies for controlling kudu and jackal rabies are required to reduce incidence in the wild.

Keywords Rabies, Wildlife, Zoonosis, Kudu, Black-backed jackal, Namibia

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Background

Rabies is an acute, almost always fatal zoonosis, and neglected tropical disease (NTD) of mammals around the world. In southern Africa, the disease is caused by the rabies virus (RABV), a neurotropic *Lyssavirus* belonging to the *Rhabdoviridae* family that is excreted in the saliva of infected animals [1]. RABV is the most frequent cause of human, domestic, and wild animal rabies worldwide [2]. It is frequently transmitted through a bite, scratch, or contact with the saliva of an infected animal [3]. Rabies manifests with non-pathognomonic neurological signs and lesions [2]. Common neurological signs in infected animals include excessive salivation, abnormal behaviour, aggression, and paralysis [2]. The infection is widespread in developing countries, especially in Africa and Asia (> 95% deaths), because of the high number of free-roaming dog populations and limited surveillance, diagnostic capacity, and control strategies [4, 5]. The majority of rabies cases (> 80%) occur in rural communities where disease awareness and access to post-exposure prophylaxis are limited to non-existent [2]. Rabies is a disease of public health importance; more than 60,000 humans die of rabies infection annually, with about 40% of these mortalities occurring in children [2]. Despite the high case fatality rate, rabies is a vaccine-preventable infection, and post-exposure prophylaxis (PEP), though costly, is available to prevent and reduce human mortalities [6].

The domestic dog (*Canis lupus familiaris*), some wild carnivores and several bat species (Chiroptera) are the natural reservoir hosts for rabies-causing viruses [2]. However, the domestic dog is the primary host and frequent source of infection for humans and animals worldwide [2]. In domestic dogs and some wild carnivores such as the black-backed jackal (*Canis mesomelas*), intraspecific transmission of host-adapted rabies virus strains is sustained [7]. In non-reservoir hosts that include most domestic and wild animals, infection occurs as a spillover from reservoir hosts. In spillover rabies infections, transmission within the infected species is often limited, leading to the eventual clearance of the infection over time [7]. In Namibia, rabies is endemic, and the causative RABV circulates within both domestic and wild animals. Free-roaming dogs are the main reservoir and source of infection in the domestic cycle [8]. Despite the implementation of free annual rabies vaccinations in dogs and cats and other rabies control measures in Namibia based on the One Health principle, human deaths persist, with over 242 deaths recorded from 2001 to 2017 [8]. Thus, rabies presents a challenge to public and animal health. In the wild, the black-backed jackal is the main reservoir and vector of rabies infection. The domestic and sylvatic cycles of rabies are linked by the respective main reservoir and vector hosts, the dog and black-backed jackal (herein called jackal). Recent evidence points to a shift of the rabies virus to new reservoir hosts [9]. In Namibia, the sustained rabies infection that has been observed to occur in Greater Kudu (*Tragelaphus strepsiceros*) [10] has led to the suspicion that Greater Kudu (referred to later as kudu) are new reservoir hosts of the virus. However, recent scientific evidence refutes this assertion and implicates canids such as the black-backed jackals and domestic dogs, as the source of infection for kudu [10].

Previous studies on rabies in Namibia have focussed mainly on domestic animals and a few wild animal species [8, 11]. Therefore, there is incomplete epidemiological information on rabies in Namibia, especially on the part of wild animals. Knowledge of the epidemiology of wild animal rabies is necessary to inform targeted prevention and control measures, and rabies elimination strategies in domestic dogs in the country. In this study, we describe the incidence, spatio-temporal dynamics, and clinical presentation of rabies infection in various wild animal species in Namibia based on records from 2001 to 2019.

Results

Overall positivity

A total of 1635 wild animal brain samples from suspected cases were submitted to the laboratory for rabies confirmation. The majority of these samples originated from kudu (59.6%, $n = 974$), followed by jackals (14.3%, $n = 234$), eland (5.3%, $n = 87$), and 49 other wild animal species (20.8%, $n = 340$) (Table 1) resident on commercial farms (69.3%, $n = 1133$), urban (23.6%, $n = 386$), wildlife protected (4.3%, $n = 71$), and communal areas (2.8%, $n = 45$). Approximately 64.8% (1059/1635) of the submitted brain samples were confirmed positive for rabies infection (Table 1) on the direct fluorescent antibody test. Using the Rogan and Gladen estimator [12], we estimated the true positive rate at 67.1% (95% CI: 64.7–70%). The positive cases comprised 33 (63.5%, 95% CI: 49.9–75.2%) wild animal species (Table 1). The total and median rabies cases varied by animal species, with 88.4% of the cases ($n = 935$) recorded in kudu ($n = 755$) and jackals ($n = 181$). Within species, positive rates for rabies were higher in kudu (77.5%, 755/974) and jackal (77.4%, 181/234) than in other species (Table 1), but this should be interpreted taking into account the variability in the sample size, with the two animal species contributing about three-quarters of the total samples tested. Regarding feeding habits, rabies cases were higher in herbivores (71.6%, $n = 827$) than in carnivores (61.3%, $n = 228$) and omnivores (10%, $n = 4$) (Table 1, $p < 0.00001$, $X^2 = 75.7754$).

The majority of rabies positive cases were reported on commercial farms (72.8%, 771/1059) (Table 2). More wild animal species tested positive for rabies on commercial farms ($n = 26$) than in urban areas ($n = 9$), communal areas ($n = 8$), and wildlife-protected areas ($n = 7$) (Table 2).

Table 1 Rabies positive rates by wild animal species, and feeding habits (carnivores, herbivores, and omnivores) (2001–2019). Wild animals (*n* = 68) in which rabies infection was not detected are indicated as **'all other species'**

Species	No. tested	% positive (*n*)	% negative (*n*)	Overall % positive (*N* = 1635)
Carnivores				
Jackal (*Canis mesomelas)*	234	77.4 (181)	22.6 (53)	11.07
Meerkat (*Suricata suricatta*)	34	11.8 (4)	88.2 (30)	0.24
Mongoose (not specified)	32	6.3 (2)	93.7 (30)	0.12
Bat-eared fox (*Otocyon megalotis*)	19	68.4 (13)	31.6 (6)	0.80
Honey badger (*Mellivora capensis*)	14	71.4 (10)	28.6 (4)	0.61
Cheetah (*Acinonyx jubatus*)	10	30 (3)	70 (7)	0.18
Hyena (Not specified)	9	44.4 (4)	55.6 (5)	0.24
African wild cat (*Felis lybica*)	5	40 (2)	60 (3)	0.12
Leopard (*Felis lybica*)	5	20 (1)	80 (4)	0.06
Aardwolf (*Proteles cristata*)	3	100 (3)	0 (0)	0.18
African wild dog (*Lycaon pictus*)	3	66.7 (2)	33.3 (1)	0.12
Lion (*Panthera leo*)	2	100 (2)	0 (0)	0.12
Caracal (*Caracal caracal*)	2	50 (1)	50 (1)	0.06
Total	**372**	**61.3 (228)**	**38.7 (144)**	13.94
Herbivores				
Kudu (*Tragelaphus strepsiceros*)	974	77.5 (755)	22.5 (219)	46.18
Eland (*Taurotragus oryx*)	87	62.1 (54)	37.9 (33)	3.30
Oryx (*Oryx gazella*)	26	3.8 (1)	96.2 (25)	0.06
Waterbuck (*Kobus ellipsiprymnus*)	10	30 (3)	70 (7)	0.18
Duiker (*Sylvicapra grimmia*)	9	22.2 (2)	77.8 (7)	0.12
Antelope (not s[ecified)	9	22.2 (2)	77.8 (7)	0.12
Squirrel (*Xerus inauris)*	9	11.1 (1)	88.9 (8)	0.06
Blue wildebeest (*Connochaetes taurinus*)	7	14.3 (1)	85.7 (6)	0.06
Giraffe (*Giraffa camelopardalis*)	5	20 (1)	80 (4)	0.06
Roan antelope (*Hippotragus equinus*)	5	20 (1)	80 (4)	0.06
Impala (*Aepyceros melampus*)	4	25 (1)	75 (3)	0.06
Dassie (*Procavia capensis*)	3	33.3 (1)	66.7 (2)	0.06
White rhinoceros (*Ceratotherium simum simum*)	3	33.3 (1)	66.7 (1)	0.06
Camel (*Camelus dromedarius*)	2	50 (1)	50 (1)	0.06
Black rhinoceros (*Diceros bicornis*)	1	100 (1)	0 (0)	0.06
Damara dik dik (*Madoqua kirkii*)	1	100 (1)	0 (0)	0.06
Total	**1155**	**71.6 (827)**	**28.4 (328)**	**50.58**
Omnivores				
Mouse (Not specified)	28	3.6 (1)	96.4 (27)	0.06
Rat (Not specified)	6	16.7 (1)	83.3 (5)	0.06
Baboon (*Papio ursinus*)	5	20 (1)	80 (4)	0.06
Raccoon (*Procyon lotor*)	1	100 (1)	0 (0)	0.06
Total	**40**	**10 (4)**	**90 (36)**	**0.24**
All other species** (*n* = 19)	**68**	**0 (0)**	**100 (100)**	**0**
Overall	**1 635**	**64.8 (1059)**	**576 (35.2)**	**64.8**

**Springbok (11), zebra (11), bat (8), sable antelope (7), monkey (6), nyala (6), steenbok (3), genet (3), warthog (2), hartebeest (2), Cape fox (1), elephant (1), Guinea pig (1), hamster (1), hare (1), lechwe (1), pangolin (1), polecat (1), skunk (1)

In the univariate analysis, only the 'land use system' was significantly associated with the number of rabies cases ($p < 0.05$). Therefore, this variable was analysed further in a multivariable generalised linear model, which revealed that the rabies cases were highest on commercial farms, followed by urban settings, and lowest in national parks (Table 3). When compared with communal areas, rabies infection was significantly higher in urban ($p = 0.011$; OR = 6.21) and commercial ($p = 0.0006$; OR = 10.95) settings (Table 3).

Geographic distribution of rabies cases

Rabies cases were reported in 12 of 14 regions of Namibia (Fig. 1). Kavango East and Kavango West regions did not submit brain samples for laboratory confirmation during the study period. Approximately 91.1% of rabies

Table 2 Rabies positive rates, and the diversity of rabies positive wild animal species detected in commercial farming, urban, wildlife protected, and communal areas

Land use	% rabies positive	Number of species positive	Species positive for rabies	
Commercial farms	72.8 (771/1059)	26	Aardwolf	African wild dog
			African wild cat	Antelope
			Baboon	**Bat-eared fox ***
			Black rhinoceros	Blue wildebeest
			Camel	Caracal
			Cheetah	Damara dik dik
			Duiker	Eland
			Giraffe	Honey badger
			Impala	**Black-backed jackal***
			Kudu*	Leopard
			Lion	Meerkat
			Mongoose	Roan antelope
			Waterbuck	
			White rhinoceros	
Urban area	19.9 (211/1059)	9	**Bat-eared fox***	Duiker
			Eland	**Black-backed jackal***
			Kudu*	Meerkat
			Mouse	Oryx
			Rat	
Wildlife protected areas	5.7 (60/1059)	7	African wild cat	**Bat-eared fox***
			Honey badger	Hyena
			Black-backed jackal*	**Kudu***
			Lion	
Communal area	1.6 (17/1059)	8	**Bat-eared fox***	Honey badger
			Hyena	**Black-backed jackal***
			kudu*	Mongoose
			Raccoon	Squirrel

*wild animal species (kudu, bat-eared fox, and jackals) in which rabies was detected in all land use systems

Table 3 A generalized linear model for association between predictor variables and incidence of rabies cases*

Variable	Category	Median no. of cases (1st and 3rd quantiles)	Standard error	Odds ratio (95% CI)	*p*-value
Land use system	Communal (ref)	0 (0, 0.5)			
	Commercial	13.5 (7, 47.3)	0.696	10.95(2.79, 42.86)	0.0006**
	National Park	0 (0, 0)	0.947	1.11(0.17, 7.12)	0.911
	Urban	4 (1, 5.8)	0.721	6.21(1.51, 25.53)	0.011**

*Analysis was conducted using a generalised linear model with Poisson distribution; **significant at $p < 0.05$

cases ($n = 965$) were recorded in five regions of Namibia (Otjozondjupa ($n = 373$), Khomas ($n = 210$), Kunene ($n = 154$), Erongo ($n = 123$)) and Omaheke ($n = 105$) (Table 4). The total and median number of rabies cases was highest in Otjozondjupa region (central Namibia) (total = 373; median = 18; range: 6–42), followed by Khomas region (central Namibia) (total = 210; median = 5; range: 1–36), Kunene region (northwest Namibia) (total = 154; median = 6; range: 1–18), and Erongo region (central-western Namibia) (total = 123; median = 4; range: 0–21) (Table 4). A similar trend was observed in kudu, with the highest number of rabies cases occurring in the central-western regions of Otjozondjupa region ($n = 294$), followed by Khomas ($n = 180$), Erongo ($n = 97$), and Kunene ($n = 61$) regions (Fig. 1). Kudu rabies was not detected in the Oshana and Zambezi regions. In jackals, the highest number of rabies cases ($n = 72$, 40%) was in the Kunene region, followed by Otjozondjupa ($n = 38$), Khomas ($n = 15$), and Erongo ($n = 12$) regions, but there were no cases in Oshana and Zambezi region (Fig. 1). Rabies cases in the eland were clustered in the Otjozondjupa region (Fig. 1).

Our findings from local Moran analysis confirmed the existence of relatively high-risk clusters of rabies in Otjozondjupa and Khomas in central Namibia, with the former cluster being significant ($p = 0.0096$) (Fig. 2; Table 4). Low-risk clusters were observed in Oshikoto and Omaheke regions in the mid-north and mid-east of Namibia, but they were surrounded by high-risk regions (Fig. 2; Table 4). The global Moran's I analysis of Monte Carlo permutations confirmed significant positive spatial autocorrelation of overall rabies cases from wild animal species in Namibia (Moran's I = 0.13; $p = 0.042$). This means that, as rabies cases in a region increase, so do the

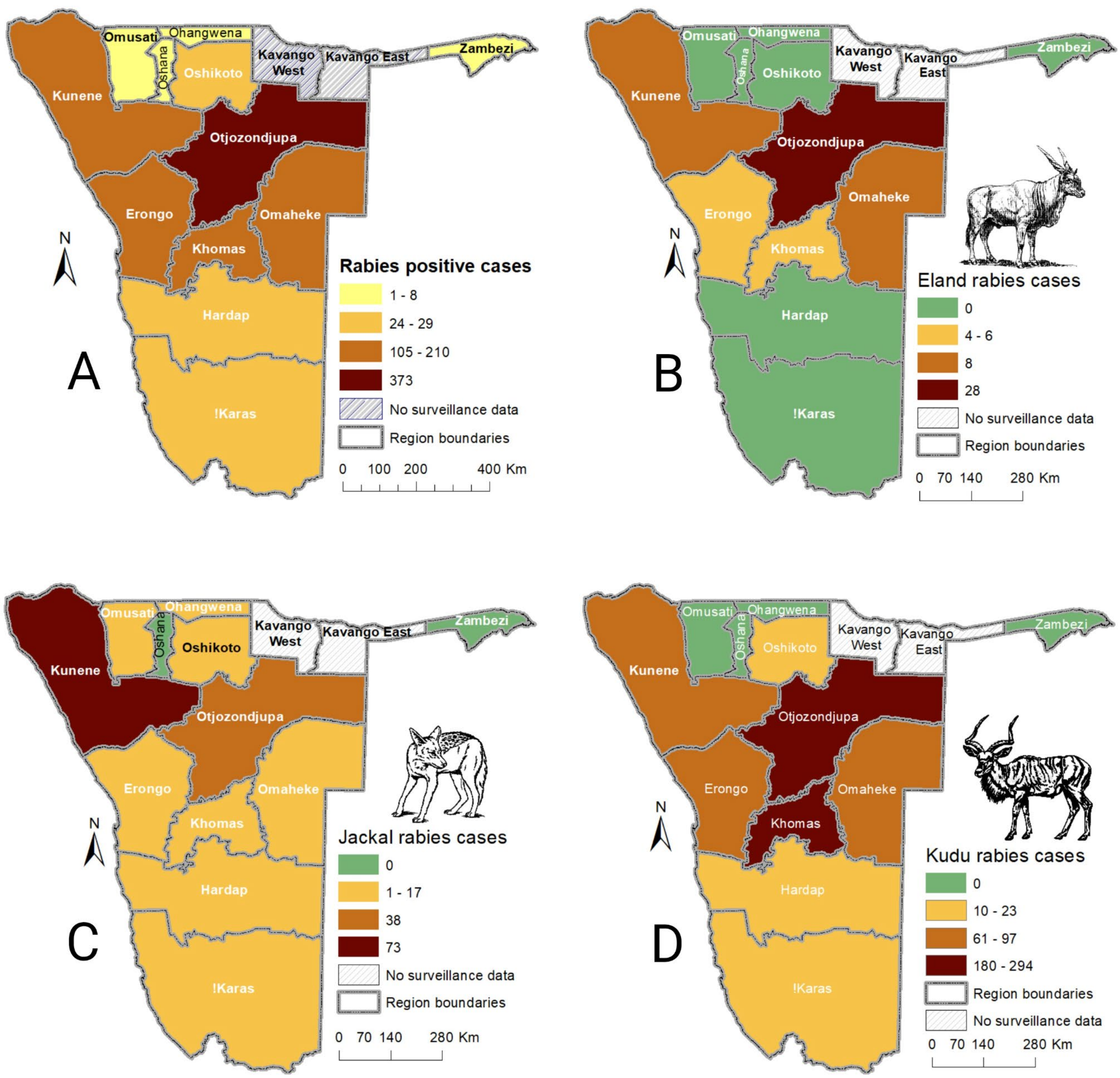

Fig. 1 Spatial distribution of total (A), eland (B), jackal (C), and kudu (D) rabies cases in Namibia (2001–2019). Rabies cases were clustered in the central-western parts of the country

cases in neighbouring regions, confirming that rabies cases were not distributed randomly across regions.

Temporal distribution of rabies cases

The cumulative number of positive rabies cases for each month from 2001 to 2019 is depicted in Fig. 3. From January to June, more rabies cases (> 96) were recorded per month. However, the number of rabies cases declined from July to December. A similar trend was observed for kudu rabies cases. In this species, rabies cases were higher from January to June, and declined until August, to maintain a relatively low but stable number of cases until December (Fig. 3). In contrast, rabies cases in jackals showed a steady rise from January to peak between May and August and declined thereafter until December. Our results show that jackal cases rose as the number of reported cases in kudu peaked. From August to December, when kudu rabies cases were at their lowest, jackal rabies cases were declining (Fig. 3).

The total annual rabies cases fluctuated over the years, with clear peaks observed in 2006, 2007, 2010, and 2013 and a general decline in cases from 2014 to 2019 (Fig. 4). The same pattern was observed for annual kudu rabies cases, but they were always higher than the cases in

Table 4 Descriptive and Moran Spatial statistics (Ii) concerning rabies cases in 52 wild animal species from 12 regions in Namibia (2001–2019)

Region	Total rabies cases	Median annual incidence of cases (range)	Ii (Ii variance)	*p*-value	Cluster classification
Zambezi	1	0 (0–1)	0.0 (0.0)	0.742	Low-low
Erongo	123	4 (0–21)	0.134 (0.0045)	0.043	High-High
Hardap	28	1 (0–10)	0.0 (0.0397)	0.923	Low-Low
Kharas	24	1 (0–4)	0.212 (0.227)	0.627	Low-Low
Khomas	210	5 (1–36)	0.238 (0.024)	0.108	High-High
Kunene	154	6 (1–18)	0.156 (0.040)	0.358	High-High
Ohangwena	3	0 (0–1)	0.397 (0.124)	0.213	Low-Low
Omaheke	105	3 (0–19)	-0.0497 (0.0007)	0.073	Low-High
Omusati	8	0 (0–2)	0.170 (0.124)	0.549	Low-Low
Oshana	1	0 (0–1)	0.204 (0.081)	0.390	Low-Low
Oshikoto	29	1 (0–11)	-0.259 (0.0397)	0.228	Low-High
Otjozondjupa	373	18 (6–42)	0.340 (0.204)	0.0096	High-High
Kavango East	No data	-	-	-	-
Kavango West	No data	-	-	-	-

jackal (Fig. 4). On average, 39.7 ± 22.4 and 9.5 ± 5.2 positive cases were recorded per year in kudu and jackal, respectively. In contrast, annual jackal rabies cases were generally low over the study period, especially from 2014 to 2019 (Fig. 4).

Clinical signs of rabies observed in infected kudu and jackal

A total of 571 kudu brain samples that tested positive for rabies antigen at the laboratory were accompanied by a description of clinical signs. The most common clinical signs were behavioural changes ($n = 441$, 77.2%) including aggression towards humans and domestic animals, tameness, approaching human and livestock areas, mingling with domestic livestock, and roaming in town. Excessive salivation (35.0%, $n = 200$); neurological signs (14.7%, $n = 84$) including head shaking, tilted head, continuous vocalisation, chewing gum fits, twitching of the lips, open mouth, wild gaze, blindness, hindquarter paresis, paralysis, ataxia, circling, disorientation, recumbency, tail wagging, paddling, and mortalities ($n = 80$, 14.0%) were also frequent clinical presentations of rabid animals. In jackal, 160 rabies-positive animals had a description of clinical signs, with 90.6% ($n = 145$) exhibiting behavioral changes, 13.1% having neurological signs ($n = 21$) and 2.5% showing excessive salivation ($n = 4$).

Wild animal bites on humans and domestic animals

A total of 95 bites were inflicted on humans (49.5%, $n = 47$), dogs (38.9%, $n = 37$), and livestock (11.6%, $n = 11$) by a variety of wild animals. Jackals were responsible for the majority (80%, 76/95) of bites recorded in this study. Other wild animal species that were involved in bites were the honey badger (8.4%, $n = 8$), Surricate (3.2%, $n = 3$), bat-eared fox (3.2%, $n = 3$), mongoose, dassie, squirrel, mouse and rat (all 1.1%, $n = 1$ each).

Discussion

In our study, the overall positive rate was 64.8%, which was lower than the positive rate of 76.4% estimated by Hikufe et al. [8] based on a smaller sample size. Positive rates among wild animals are projected to be higher because passive surveillance for rabies is less intense, and in situations where more than one animal is suspected, only one brain sample may be sent for testing at the laboratory. In addition, wild animals with rabies cases are difficult to detect on vast tracts of land where rabid animals are preyed upon very quickly, and this potentially explains the low positivity of rabies cases (game parks) in wildlife protected areas. Our study showed that rabies infection affects a wider range ($n = 33$) of wild animal species in Namibia than previously reported [8]. A wide mammalian host range for the rabies virus [13–15] as reported in our study is a potential threat to domestic animal and human health, and the eradication of dog-mediated rabies from Namibia.

A higher proportion of suspect rabies samples (69.3%), and positive cases (72.8%) handled at the laboratories were from commercial farming areas than other land use systems, as was also noted by Hikufe et al. [8]. Farmers on these fenced, mainly game hunting farms, have the capability and motivation to carry out voluntary rabies surveillance [8]. The rearing of game species on these freehold farms follows a conservation approach that promotes the proliferation and high density of wild animal species, and the rapid spread of rabies infection. The high positive rates recorded on commercial farms have implications on the health of sympatric domestic animals on mixed farms, and humans that come into contact with these animals.

The majority of rabies cases were recorded in herbivores (827/1059), the predominant wild animal species on freehold farms. Among herbivores, kudu rabies was

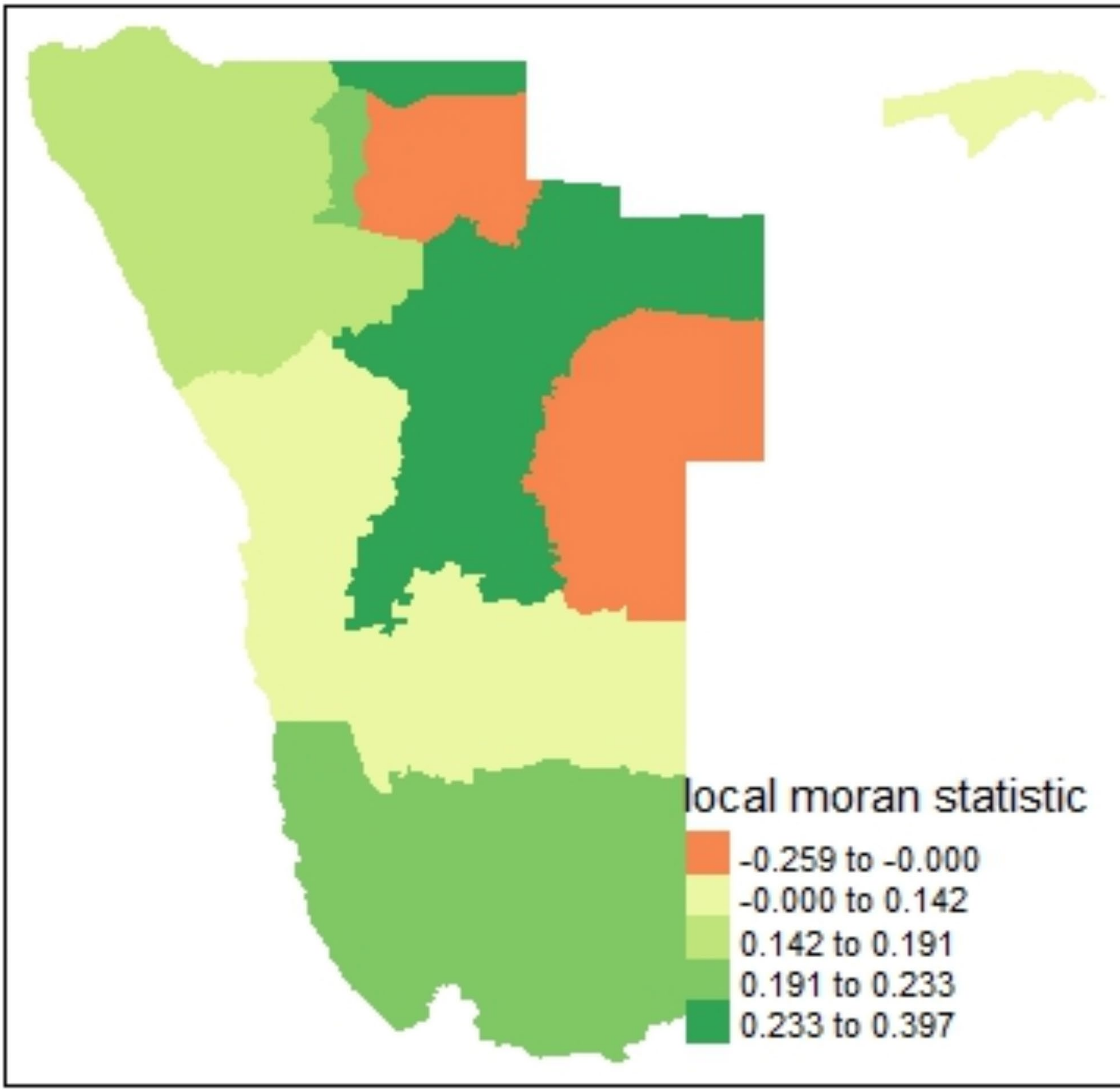

Fig. 2 Local Moran's I cluster map for rabies cases in 52 wild animal species in Namibia (2001–2019)

dominant (77.5%, 755/974) as reported previously [8, 11, 16]. Due to their larger size and gregarious nature, clinical signs of rabies are easily detected in herbivores than in carnivores or omnivores which live in smaller or solitary groups. Kudu rabies has been prominent for several years on commercial farms in Namibia. At current knowledge, there is no proven explanation for the high susceptibility and number of rabies cases in kudu in Namibia. In the past, horizontal transmission (non-bite) of a genetically distinct RABV that is sustained within the kudu population was put forward as a mode of transmission [16–19] and maintenance of the rabies cycle in kudu [20, 21]. However, results of molecular studies suggest that the rabies viruses isolated from kudu and jackal are genetically related and that kudu and jackal are part of one epidemiological cycle of rabies [22]. Independently maintained RABV strains in Namibian greater kudu have been attributed to domestic dogs, via their interactions with predators such as the black-backed jackal (*C. mesomelas*), which were originally infected by domestic dogs [23, 24]. Jackals and bat-eared foxes are presumed to be more effective reservoirs and vectors of rabies infection for other animals sharing the same space than kudu [8]. The high population density of kudus in Namibia increases

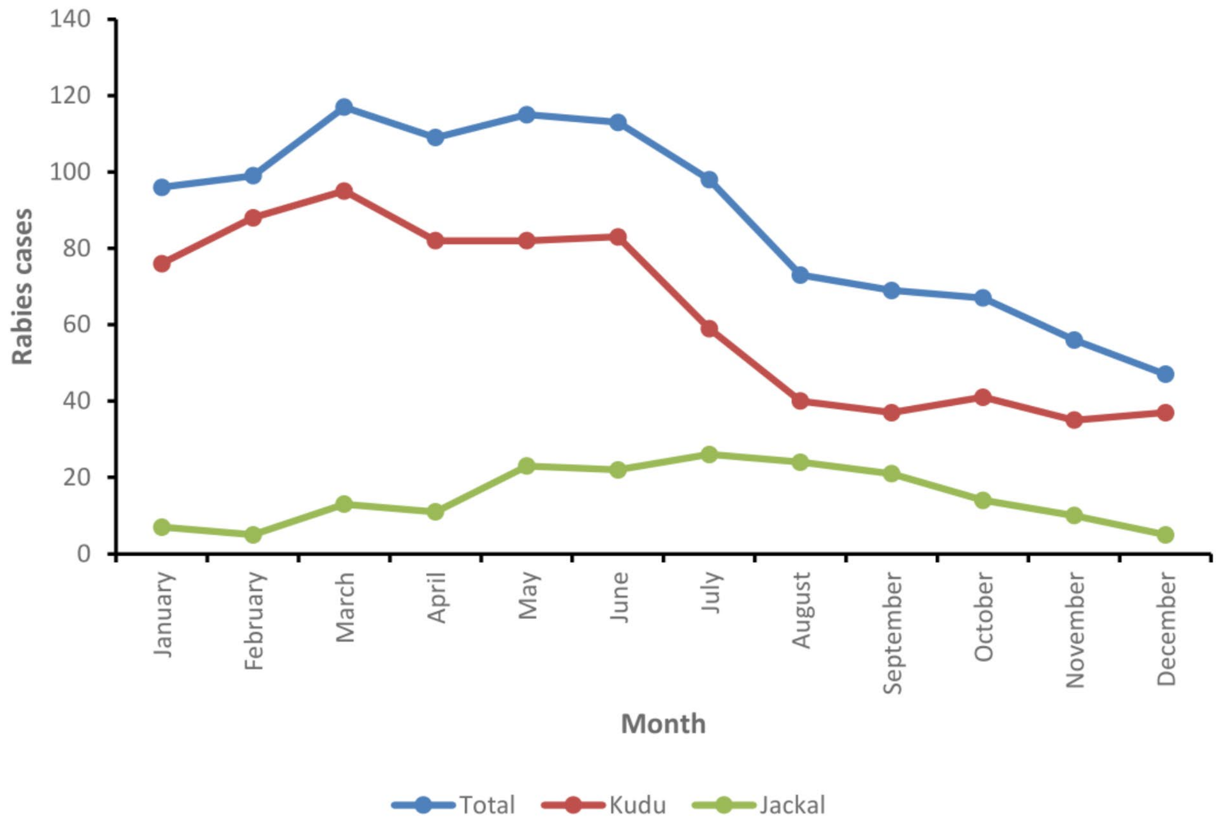

Fig. 3 Monthly trends of total, kudu, and jackal rabies cases (2001–2019)

their exposure to rabies virus from a variety of predator animals, even those in relatively low populations or less effective reservoirs. This promotes rapid rabies transmission and the resultant epidemics that are a feature of kudu rabies [16] and may explain how jackals interact with and transmit rabies infection to kudu, even though they are not their primary prey species. Our study identified the eland as the second most important herbivore in the country for rabies infection. Unlike in kudu, rabies infection in other herbivores showed a typical spillover type of infection where the infection is short-lived within the species resulting in a few cases recorded over the 19-year study period. From a public health perspective, it is encouraging that direct transmission of rabies infection from wild herbivores such as kudu to humans has not been documented in Namibia [25].

Among carnivores, jackals, bat-eared foxes, and honey badgers presented the highest numbers and relatively high percentage of confirmed rabies cases, with no significant difference in their proportion of cases. The positive rate was higher than 65% in each of the three species, and this poses a high risk to their populations in the conservation areas and a transmission risk to other wildlife species, especially their prey. Previous studies in Namibia have also reported high positive rates of rabies in jackals (87%) [8]. Based on the number of cases reported, our study confirms the jackal as the second major wild animal species affected by rabies in Namibia. In jackals, rabies is a major cause of mortality, and they are a well-documented major reservoir and vector for rabies infection in wild and domestic animals [26]. It is believed that jackals are responsible for transmitting rabies to most wild animal species [16], and this is further fostered by their relatively high population in the wild compared to the other carnivore species such as bat-eared foxes and honey badgers. In our study, this assertion is confirmed by the fact that rabid jackals were responsible for the majority of bites (80%) observed in livestock, dogs, and humans. Data on jackals biting wild animals was not available. However, we presume that the number of wild animals bitten by rabid jackals is higher than that in domestic animals due to proximity. Our findings are in contrast to the wildlife rabies epidemiological picture in South Africa, where yellow mongoose (*Cynictis penicillata*) rabies dominated (35.5%), followed by bat-eared fox (*Otocyon megalotis*) (20.5%), and black-backed jackal (*Canis mesomelas*) (15.5%) infections [27]. We suspect that the rabies cases reported in other carnivores in our study are spillover infections from either jackals or domestic dogs. A molecular characterization study of virus isolates

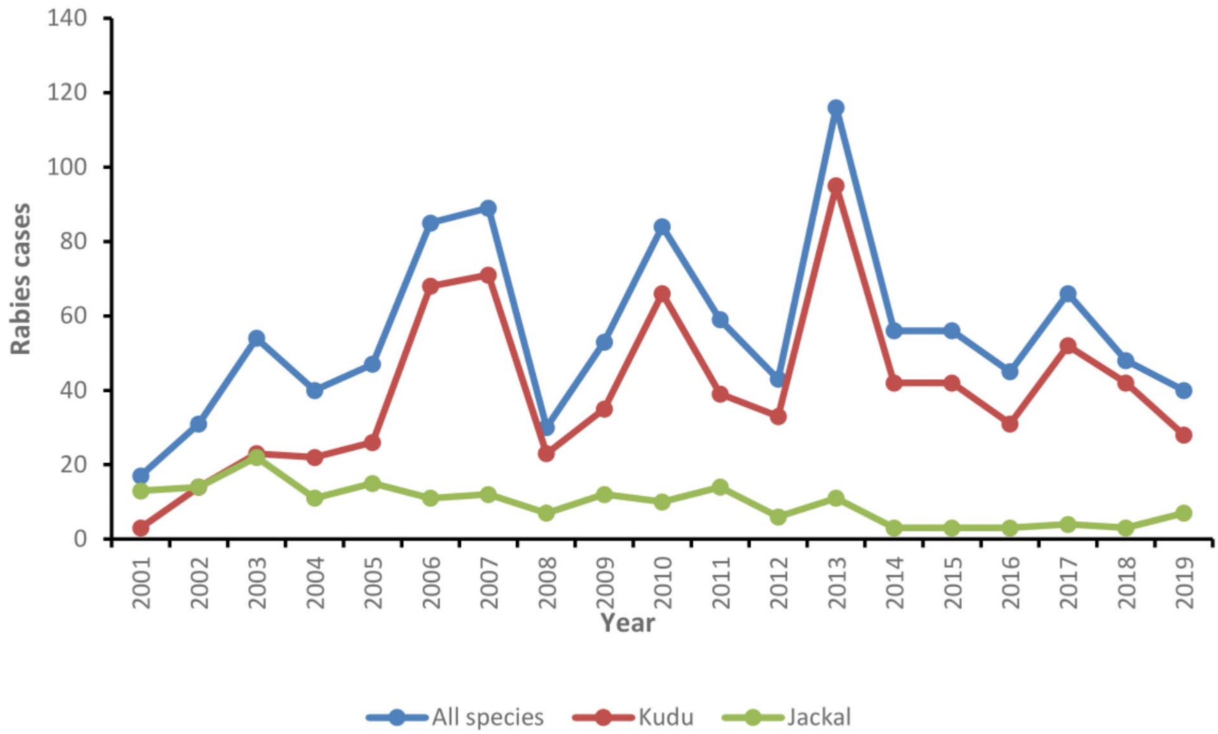

Fig. 4 Annual trends of total, kudu and jackal rabies cases (2001–2019)

from different species is necessary to confirm this assertion. Few cases ($n=4$) were recorded among omnivores including the raccoon, baboon, mouse, and rat; perhaps an indication of the little contact they have with the major reservoirs, but also the lower level of surveillance in these species [28].

In terms of geographical spread, wild animal rabies cases were detected in all but the two regions of Kavango East and Kavango West. In these regions, no surveillance data was collected over the study period. However, rabies cases are presumed to occur in the two regions as evidenced by the highest number of human rabies cases that have been previously reported [8]. Proximity to, or harboring a wildlife protected area or commercial farm was associated with a high number of rabies cases as was observed in the central and north-western regions of the country (Otjozondjupa, Khomas, Erongo, Kunene, and Omaheke). The distribution of rabies cases followed the major habitats of kudu in the country as has been reported previously in Namibia [29, 30]. Thus, rabies cases were clustered in regions with a dominance of kudu on farms (Otjozondjupa, Khomas, Kunene, and Erongo). As expected, there were no kudu and other wild animal rabies cases reported in the northern communal regions of Ohangwena, Omusati, and Oshana. The low proportion of suspected and positive cases in the northern communal areas is in line with the low numbers of wild animals, the low intensity of surveillance [8], fragmented to non-existent wild animal habitats, and few conservation efforts in the communal areas. Despite the Zambezi region's location in the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA), where wild animals (including kudu) roam freely across international borders, no cases of rabies were reported. Jackal rabies cases were spread around the country, but like in kudu, cases were clustered in freehold areas, as has also been observed in Zimbabwe [26]. Although rabies cases in bat-eared foxes were few, their spatial distribution covered all land use systems, suggesting that this species' role may not be ignored. The Kunene region in which the Etosha National Park is located, had surprisingly fewer cases of kudu rabies than the aforementioned regions due to the inherently low to absent disease surveillance in conservation areas. Despite hosting large numbers and a great variety of wild animal species, wildlife protected areas had sporadic submissions of suspect rabies cases, and low numbers of confirmed rabies cases (4.3%, 5.7%). This is in line with the absence of planned and coordinated disease surveillance in wildlife-protected areas, where the objective is to keep external interference as low as possible. Moreover, it is difficult to detect rabies cases in such vast lands where live or dead rabid animals are prone to predation. Therefore, the number of wild animal rabies cases reported for wildlife protected areas is likely an underestimation. However, Rottcher and Sawchuk [31], Foggin [32], and Bingham et al. [33] contend that it is difficult for rabies infection to be established and sustained in protected areas, where a large variety of wild animal species co-exist. It is suggested that the diversity of wild animal species prohibits any one carnivore species from becoming so numerous as to promote interspecies contact and sustain the infection [32]. Based on the high number of cases recorded, wild animal rabies surveillance, prevention, and control efforts should be targeted at the central-western regions of the country.

Unsurprisingly, more suspect and positive cases were recorded in urban areas (23.6%, 19.9%) than in protected areas (4.3%, 5.7%) and communal areas (2.8%, 1.6%). The cases in urban areas, being mainly from kudu, arose from affected animals that strayed into urban areas from the surrounding freehold farms. Most urban areas in Namibia are surrounded by freehold commercial livestock and wild animal farms that have a higher capacity and intensity for disease surveillance than wildlife protected areas and communal areas. As has been established, rabid wild animals roam into human settlements including urban areas, where they may spread rabies infection through contact and attacks on domestic dogs and humans [34, 35]. The contribution of spillover infections from the domestic dog population in urban areas to wild animals on surrounding farms cannot be excluded.

Our findings show that the sylvatic cycle of rabies was more of a concern on freehold farms than on other land use systems, and that kudu followed by jackal rabies was dominant in these areas. As a result, wild animals on freehold land can transmit the infection to sympatric livestock species such as cattle, sheep, and goats, which raises the need for regular surveillance, control, and prevention measures in domestic animal species.

A seasonal trend was observed for total wild animal (January - July) and kudu (January - June) rabies cases. Similar reports of seasonality in rabies cases have been reported previously in wild animals [8] and kudu rabies cases [29] in Namibia. A high number of rabies cases fell within a period that encompasses a part of the rainy season (January - April), hunting season (February–November), kudu breeding (April - July), and calving (January - February). The influence of these factors on kudu rabies seasonal dynamics is a subject of future studies. Contrastingly, rabies cases in jackals peaked between May and September (dry season), in line with the peak breeding (May - August) and whelping seasons for jackals. Given the incubation period of 2–12 months for rabies, we postulate that the peak in jackal rabies cases is responsible for outbreaks of rabies in kudu during the wet season in Namibia. In Zimbabwe, the apparent seasonality of rabies infection in jackals was attributed to increasing numbers of mobile juvenile jackals [33], and high jackal population densities [32], which facilitated rapid intra-species and interspecies transmission of rabies. One interesting finding from this study was the apparent relationship between kudu and jackal rabies cases in a year. We observed that as the rabies cases in kudu peaked (January to June), the cases in jackal were rising. However, when the kudu rabies cases were at their lowest, the cases in jackal were declining. Further studies are required to validate this assertion. Annually, the overall number of rabies cases showed a declining trend from 2017 to 2019 despite increased surveillance intensity, which may be a reflection of intensified and consistent country-wide rabies vaccination and awareness campaigns carried out in recent years.

Clinical signs typical of rabies infection as previously established in domestic animals were described in rabies-positive cases. It was interesting to note that rabid wild animals such as kudu and jackal almost always approached human settlements and mingled with domestic animals, increasing the chances of infection in these species. Barnard [23] also noted this phenomenon in jackals. Farmers, and tourists in particular, need to be educated on the clinical signs of rabies to prevent infection as some individuals may be tempted to play with, handle, rescue, treat tame or trapped wild animals without adequate protective gear. Our study established that behavioral changes were the most common clinical sign associated with positive rabies cases in kudu, which is in contrast to Barnard et al. [18], who identified hyper-salivation as the most typical clinical sign of rabies in kudu.

Namibia has implemented a rabies elimination strategy based on One Health principles since 2016. This involves the active participation of stakeholders from the Ministry of Agriculture, Water and Land Reform (MAWLR); Ministry of Health and Social Services (MHSS); University of Namibia (UNAM); national and international organizations [36] including the World Organisation for Animal Health (WOAH), Global Alliance for Rabies Control (GARC), and the Friedrich-Loeffler-Institute (FLI), Germany. The Global Strategic Agreement and Plan to End Human Deaths from dog-mediated rabies by the year 2030 is a noble strategy, but its objectives may not be achieved if wildlife rabies is not controlled at the human-wildlife-domestic animal interface. Control of rabies in wild animals is necessary to prevent the reintroduction or spillover of infection once it is controlled in the domestic animal population. The potential public and veterinary health impact, as well as the impact of rabies on the conservation of species, provide the rationale for controlling RABV circulation in the wild [37]. Despite its challenges, pre-exposure vaccination of kudu against rabies is justified by the observed high mortality, and potential economic losses to the tourism industry [16], hence its trial in Namibia. Given their significant role as reservoirs and vectors of rabies in the wild, the use of baited rabies vaccines in jackals in Namibia is recommended. However, large-scale vaccination of dogs remains an effective approach for curtailing the spread of domestic canine RABV to wild animals [38] and other species [28] and eliminating rabies within the primary reservoir (dog). Our results revealed that rabies control measures in Namibia need to be targeted at kudu in freehold farming areas and that an integrated One Health approach involving collaboration among animal health, human health, environmental, and wildlife sectors is necessary for rabies control. Adoption of routine molecular typing of RABV strains can also provide valuable data for identifying reservoirs of infection and for epidemiological tracing during outbreaks.

The study had some limitations. There was a large variability in the sample size according to animal species, which may affect better understanding of the epidemiological situation. Moreover, the study was based on data collected through passive surveillance; likely some wild animal rabies cases were not reported resulting in the underestimation of cases in the country and regions. Data on the age and sex of rabid animals was missing, which made it impossible to link these factors to the infection. We could not find the recent estimates of wild animal populations in the country to permit the estimation of prevalence and assess the threat of rabies infection to wildlife conservation. However, the data helped to identify specific wild animal species and areas requiring targeted rabies control in the country.

Conclusion

This study showed that rabies affects several wild animal species in Namibia. Kudu and jackal were the major wild animal species that tested positive for rabies infection. Most wild animal rabies cases were in kudu on commercial farms in the central regions of Namibia, with Otjozondjupa being a significant high-risk cluster for rabies. Therefore, commercial farms should be a target for wild animal rabies control in Namibia. Regions with many rabies cases influenced the number of cases in neighbouring regions. The high positive rate in kudu and jackals and their relatively high population densities in the wild threatens the sustainable conservation of these species.

Materials and methods

Study area

Namibia is located in the southwestern part of Africa at coordinates 22°58'1.42"S and 18°29'34.80"E. It shares borders with Angola to the north, South Africa to the south, and Botswana and Zimbabwe to the east. It is a sparsely inhabited country with a human population of 3,022,401 people [39] and a population density of 3.11 people per square kilometre due to its semi-arid and arid climate [40]. The country is divided into 14 administrative regions (Fig. 1). Most wild animals live in wildlife-protected areas such as national parks, game reserves, and conservancies, as well as on freehold farms, which are purely game farms or rear both game and domestic animal species such as cattle, sheep, or goats in a mixed farming system.

Study design and data collection

Wild animal rabies surveillance in Namibia is based on reports of suspect cases and brain samples submitted to the state veterinary services by veterinarians, paraprofessionals, farmers, and members of the public. In particular, wild animals (especially kudu, jackal, and other carnivores) that die of unknown causes are sampled and tested for rabies infection. Clinical cases of wild animal rabies are observed in the field based on clinical signs such as behavioural change, excessive salivation, hydrophobia, attacking and biting at imaginary objects (fly biting), weakness, or paralysis. These are humanely killed, and intact heads or brain tissue are preserved, placed in secure, clearly marked, leak-proof packaging, and dispatched to the Central Veterinary Laboratory (Windhoek) or the Ondangwa Veterinary Laboratory for confirmation of rabies infection. Surveillance data and results thereof are stored centrally at the Epidemiology Section of the Directorate of Veterinary Services [8].

In this retrospective study, we analyzed wild animal rabies surveillance data (1 January 2001 to 31 December 2019 inclusive) that were obtained from the Directorate of Veterinary Services (Epidemiology Section), with the permission of the Chief Veterinary Officer. The data comprised suspect clinical and post-mortem cases whose brain specimens were sampled, and submitted to one of the two veterinary laboratories in the country for confirmation of rabies infection. The samples had been subjected to the direct fluorescent antibody (DFA) test, which is the standard confirmatory test for rabies. The DFA test was performed as per the WOAH recommended protocol [2] following appropriate biosafety and containment procedures in a BSL-2 laboratory by personnel who had received full pre-exposure prophylaxis against rabies. After filtering and cleaning, the data comprised the following content: date of sample submission; farm name and number; GPS (global positioning system) coordinates of the farm/ place of sampling; region of origin; veterinary district of origin; animal species; clinical signs, and rabies test result (positive or negative). Suspect clinical cases not subjected to laboratory confirmatory testing and duplicates were excluded from the study. A case of rabies was considered as an animal whose brain sample tested positive for rabies antigen at the laboratory.

Statistical analysis

Data was collated, sorted, and analyzed using descriptive statistics. Proportions of rabies cases were calculated per species, feeding habits, and land use system (commercial farms, communal areas, protected areas, and urban areas). Descriptive statistics were performed to establish the medians and range of fluorescent antibody test (IFT)-confirmed rabies by wild animal species at regional and national levels. Temporal patterns were determined by month and year. Proportions were calculated to determine the most frequent clinical signs associated with positive cases in various wild animal species. The Chi-squared test of association was used to test the relationship between variables, with $p < 0.05$ as the significance level.

We assessed the association between the incidence of rabies cases and three variables: animal species, geographical region, and land use system, in univariate and multivariable generalised linear models (GLM). The GLM employed a Poisson distribution. Only kudu and jackal, which contributed a big proportion of the total rabies cases, were considered for this analysis. The rabies data were log-transformed first to normalize distribution, and only variables with $p < 0.05$ from univariate analysis were included in the final model.

For hypothesis testing, rabies cases in Namibia were aggregated for all animal species for the study period because the number of cases was too low for animal species and temporal segregation. Therefore, the unit of assessment was aggregated DFA-confirmed cases (median annual incidence) in all wild animal species by region in Namibia. The shape file of Namibia's regions was obtained from an open source [41] and edited in QGIS desktop version 3.38.15. Choropleth maps of rabies incidence were generated by wild animal species for the study period (2001 to 2019).

Spatial analytical tools were applied to examine the overall patterns of rabies in specific areas without focusing on exact locations (global level) and small-scale patterns of wild animal rabies cases across the study area (local level), as previously described [42, 43]. The global Moran's index (I) analysis was implemented to determine significant spatial autocorrelation of rabies cases, first by defining contiguous neighbouring polygons using the "queen" spatial weight [42, 43]. This was to test the hypothesis that there was spatial clustering across Namibia by generating estimates of clustering for the entire country. Statistical significance was assessed using the Monte Carlo method with 999 replications, and the null hypothesis (no clustering) was rejected when the simulated significance level was less than 0.05. Local spatial Moran autocorrelation analysis was then conducted to determine locations where the clustering of rabies cases in wild animals was significant, using the queen spatial weights [44, 45]. The hypothesis was that rabies cases are randomly distributed across regions in a completely random process. This local Moran analysis generated estimates for each region in the rabies dataset. The presence and statistical significance of local clustering in high and low rabies risk regions were visualised using the local Moran significance maps [44]. Display of maps was done in R statistical software version 4.4.1 [46], using the packages "sf" [47], "spdep" [48], and "tmap" [49].

Abbreviations

NTD	Neglected tropical disease (NTD)
RABV	Rabies virus (RABV)
PEP	Post-exposure prophylaxis
WOAH	World Organisation for Animal Health (WOAH)
FMD	Foot-and-Mouth disease
DFA	Direct fluorescent antibody
BSL	Biosafety level
KAZA TFCA	Kavango Zambezi Transfrontier Conservation Area
MAWLR	Ministry of Agriculture, Water and Land Reform
MHSS	Ministry of Health and Social Services
UNAM	University of Namibia
GARC	Global Alliance for Rabies Control
FLI	Friedrich-Loeffler-Institute
CVL	Central Veterinary Laboratory

Acknowledgements

The Chief Veterinary Officer (Namibia) gave access to the data used in this study. The University of Namibia provided the time required to work on the manuscript.

Author contributions

O.M. conceptualised the study. E.H.H. retrieved the data. OM performed data curation. C.B., O.M., and M.S.L. analysed the data and presented the results of the study. O.M., S.C., E.M., and E.M.M. drafted the original manuscript. All authors reviewed, edited, and approved the final manuscript.

Funding

This research was self-funded.

Data availability

All data is provided within the manuscript. Other datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Ethical approval was not required as the study was based on retrospective data.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Received: 24 November 2024 / Accepted: 19 March 2025
Published online: 31 March 2025

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