# Novel rabies outbreak in a marine mammal - the Cape fur seal

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# Abstract

Rabies is the oldest documented fatal zoonotic disease, spread between mammals through infected saliva. Outbreaks have only been documented for terrestrial species, with disease risk for marine mammals rarely considered. In June 2024, rabies was confirmed in a marine top predator, the Cape fur seal (CFS, *Arctocephalus pusillus pusillus*). We provide the context and timeline of rabies detection following mounting reports of seal aggression, whereby inter-species (seal to domestic dog) transmission prompted diagnostic testing of CFS in South Africa. Laboratory-confirmed cases (n = 94) conservatively date the outbreak in CFS to August 2022; rabies has since been declared endemic to CFS. Aberrant behaviour, hyper-aggression, elevated injury prevalence and confirmation of *in-utero* transplacental infection were found in this wide ranging, amphibious, highly gregarious and abundant species. Spatio-temporal overlap with vagrant sub-Antarctic pinnipeds makes spillover to other marine mammals possible, creating a subsequent gateway for rabies transmission to Subantarctic Islands and Antarctica, currently rabies-free. At least 135 people have been bitten by suspected or confirmed rabid seals, most receiving post-exposure prophylaxis. Rabies detection in CFS increased between 2022 and 2025 in both diagnostic and systematic surveillance sampling. This suggests an outbreak which is still in an active expansion phase. Considering the tri-partite alliance (FAO-WOAH-WHO) target of zero dog-mediated rabies by 2030, the increasing number of seal attacks towards dogs, and humans raise urgent considerations that should be addressed under One Health.


# INTRODUCTION

Rabies is a highly fatal zoonotic disease spread through saliva and is caused by one of several strains of the *Lyssavirus* genus, all of which belong to the *Rhabdoviridae* family [1]. Viral shedding into the saliva enables transmission through bite wounds, licks or scratches [2] with infection through mucous membranes of the mouth, eyes and nasal passages also possible [3]. As a neurotropic virus, rabies remains diagnostically and symptomatically undetectable in the body until it moves via the peripheral nerves, into the central nervous system (CNS), where it disseminates throughout the neural parenchyma, causing encephalomyelitis and death [4]. First documented 4000 years ago, rabies is one of the oldest known infectious diseases [5,6], endemic to all continents except Antarctica [2]. Vaccination has successfully resulted in total or near-total eradication of rabies in domestic animals across North America and much of Europe [7,8]. However, 59,000 human fatalities are estimated per annum across Africa and Asia, mostly through domesticated dog transmission [9].

All mammalian species are considered susceptible to *Lyssavirus*, yet until recently only two cases of rabies had been confirmed in marine mammals: a single ringed seal (*Pusa bispida*, [10]) and a single polar bear (*Ursus maritimus*, [11]). No subsequent cases were reported in the following 30 years, as such rabies has not been considered a significant disease risk to marine species [12–14]. However, following a spate of aggressive incidents involving Cape fur seal (CFS, *Arctocephalus pusillus pusillus*) along the coast of South Africa, we now document the first wide-ranging outbreak of rabies in a marine mammal.

CFS are large, highly mobile, long-lived and charismatic marine mammals, with a continuous distribution from southern Angola to Algoa Bay, South Africa (~ 3,000 km). With approximately 1.5 to 2 million individuals distributed amongst 40 island and mainland breeding colonies, the population is considered stable [15,16] and is listed as Least Concern on the International Union for Conservation of Nature Red List (IUCN) Red List [17]. As adaptable generalist feeders, their range of prey items is diverse, and although CFS demonstrate strong site fidelity [18], foraging trips are often long and far ranging, with adult females averaging five to nine day excursions, travelling up to 140 km from their colonies [18–20]. At least for the period 1972–1993, population increase was largely attributed to the formation and expansion of mainland colonies, particularly at the northern end of their distribution[16]. However, most mainland colonies are frequented by predators, including black-backed jackal (*Lupulella mesomelas*) and brown hyena (*Hyaena brunnea*), that prey on seals (particularly pups) and scavenge on carcasses [21,22]. Both are significant reservoir species for the endemic circulation of the wild-canid rabies biotype [12,23]. Inter-species interactions provide ample opportunity for rabies virus host shift events from terrestrial carnivores to marine mammals. We present evidence of the first ever such a shift to Cape fur seals. This novel shift is an important public health concern due to the frequent interactions between Cape fur seals and humans both in water and on land. Our paper provides important insights crucial for outbreak response planning, and intervention development.

## The Road to Rabies

A broad investigation into seal health was initiated in the austral summer of 2021, following an unusual mortality event (UME) along the coast of South Africa, which prompted a spike in public and stakeholder interest in seal health and greater coordination in CFS stranding networks. From October 2021 onwards, gradually increasing reports of CFS hyperactivity and aggression, including unprovoked attacks on water users and domestic dogs, became indicative of an underlying neurological disease process. A preliminary histological report, released early in 2024, of 20 CFS brains and eight hearts sampled between December 2021 and August 2022 suggested multiple disease processes were likely affecting CFS in South Africa. Morbillivirus and rabies were uplisted as differential diagnoses for the observed changes in seal behaviour over the preceding three years. However, it was the coupling of two high-profile incidents involving CFS in Cape Town, amid mounting reports of seal aggression along the South African coastline, which expedited rabies testing of CFS.

On May 26th, 2024, a prolonged in-water attack on surfers by a juvenile CFS at the popular Muizenberg beach, Cape Town, was widely reported on social media. Between 09:00 hr and 12:00 hr, the seal was observed acting erratically and aggressively, biting several surfboards and injuring water users. It was caught and subsequently restrained for 45 minutes with a surfboard leash, during which time the seal died. A post-mortem examination revealed blunt force trauma to the dorsal cranium but no signs of death by asphyxiation. Just 48 hours later (on May 27th), reports of a dog with rabies in Cape Town were released, the first case in a domestic canine for 18 months in the Western Cape Province [24], amid speculation of rabies transmission from a seal (see Supp 1, Case Report).

Given the high human health risk that rabies presents and the suggestion of seal-mediated rabies transmission, CFS brain samples collected in May 2024 as part of the ongoing seal health monitoring were submitted for diagnostic rabies testing. Four seals recovered from the Cape Town Municipal area in May 2024 were selected. Each had an unusual case history - all were found alive and in good body condition yet presented with injuries and/or abnormal or hyper-aggressive behaviour. Of these, one (20240522 Big Bay) tested positive for rabies by duplicate brain samples using the direct fluorescent antibody test (dFAT) on freshly frozen tissue [25,26] and immunoperoxidase (IMP) staining of formalin-fixed tissue [27] (Extended Results Fig. 1). Two others, including the Muizenberg animal described above, were positive through IMP testing only, as no fresh tissue was available for dFAT testing. The fourth animal (a pregnant adult female) was negative through IMP. She had live-stranded at Kommetjie Beach with severe facial injuries (Fig. 1).

These novel results expedited the investigation of rabies in CFS using a variety of data streams, notably the retrospective assessment of 138 formalin-fixed brain tissue samples collected before June 2024 which were fast-tracked for testing. Testing was conducted through IMP staining of the hippocampal region of brains which were already prepared for histopathological assessment for a study of domoic acid (DA) toxicosis in CFS. Following June 2024, fresh brain tissue (various regions of the cortex, cerebellum and brain stem) was routinely collected from CFS in South Africa, and high-priority cases, i.e., those CFS exhibiting abnormal behaviour and confirmed human or dog contact, were submitted for diagnostic testing through dFAT (turnaround time +/- seven days). Low priority cases (i.e., pups or carcasses with no case history) were tested with dFAT and/or IMP in batches. A case history was collated for each animal tested, including standard demographic and biological information, as well as any observational reports and video footage of the animal’s behaviour (Suppl. 2 a,b).

# Disease History

The first laboratory-confirmed dFAT rabies positive case was a sub-adult bull (standard length, SL = 125 cm, Fig. 1a), caught at Big Bay beach on May 22nd, 2024, after exhibiting hyper-aggressive behaviour towards people and dogs. The aggressive state continued unabated during transit, with the animal biting the metal bars of the cage shortly before it died. Gross postmortem examination findings included congested conjunctival mucous membranes, a fractured right mandibular molar tooth and puncture wounds on both sides of the mouth and ventral mandible. Multifocal subcutaneous ecchymoses were noted on the dorsal cranium extending caudally from the orbital sockets to the parietal bone. Similar lesions were also observed in the subcutis over the right lateral thoracic wall.

The earliest positive rabies case confirmed by retrospective IMP testing of formalin-fixed brain tissues, dates from August 5th, 2022. This adult female CFS (SL = 141 cm), which startled and bit an elderly woman walking on Kommetjie Beach, was caught for observation but died in transit. The seal was lactating, not pregnant, and her stomach was full of kelp, which is abnormal for CFS. The bite victim received an incomplete course of post-exposure prophylaxis (PEP), consisting of a single rabies vaccination but without administration of human rabies immunoglobulin (RIG). She has not since developed clinical rabies.

## Rabies in Pups

Transplacental transmission of rabies is rare, though previously reported in humans [28], domestic animals [29] and wildlife [30,31]. Three pregnant adult female CFS tested positive for rabies through dFAT. From these, one carried a male foetus (est. gestation seven months, 20240925 Mossel Bay) which also tested rabies positive through dFAT, indicating transplacental transmission of rabies from cow to offspring (Fig. 1d). Of the 43 neonates tested (i.e., those born in November and December, < 1 month of age), none were conclusively rabies positive. One case, a neonate sampled in November at the Northern Cape Kleinzee colony (20241108 Kleinzee), was inconclusive through IMP (see below). Of the 15 pups tested in the one-to-six-month age range - three (20%) were rabies positive. The youngest was a pre-molt pup of estimated two to three months of age (20250220 Hout Bay). This animal was retrieved in the water by a domestic dog and held in the mouth as the dog swam in Hout Bay harbour. When released, the seal pup came ashore and walked up the boating slipway, showing little aversion to the observing crowd of adults and children (Suppl. 2a). It subsequently died in human care within 24 hrs of stranding.

## Epidemiology of Rabies in Cape Fur Seals

The geographic distribution of CFS sampling effort was widespread but not uniform, and highest along the west coast and during 2024. Rabies-positive animals were found in both the Northern and Western Cape Provinces from Kleinsee to Plettenberg Bay (Fig. 2). A single CFS in the Eastern Cape (20231027 Jeffreys Bay) displayed behavioural characteristics strongly indicative of the disease (see case definition below) but could not be tested. Of the 366 CFS tested for rabies between November 2021 and October 2025, 94 (26% of all animals tested) were rabies positive by dFAT (cases sampled falling within the case definition of suspect rabies, n = 83/94), IMP (retrospective testing of formalin-fixed brain samples from random opportunistic necropsies prior to the index cases in May 2024, n = 7/94) or duplicate samples (including the index cases in May 2024) tested with both methods (n = 4/94) (Suppl. Figure 1). A further 11 samples were inconclusive as the IMP findings showed sparse non-neuronal, but typical positive labelling of vascular endothelial cells and intravascular leukocytes in the brain tissue. The pathogenesis and relevance of this finding require further investigation.

Genome sequencing of the rabies RNA strain was conducted by the Agricultural Research Council - Onderstepoort Veterinary Research (ARC-261 OVR) [32]. The viral strain of the first dFAT rabies positive animal (20240522 Big Bay) identified through phylogenetic clustered with the black-backed jackal rabies biotype, a canid strain [27,32]. With one exception, all viral sequences derived from CFS sampled from the Northern and Western Cape between May 2024 and October 2024 showed 100% sequence identity, indicative of a single source of infection followed by intra-species transmission between CFS, which is supported by observational videos of rabid CFS attacking and biting multiple individuals during colony surveillance (authors' unpublished data, Suppl. 1b). Importantly, the viral sequence isolated from the initial rabies-positive domestic dog was similar to that sequenced from infected CFS, supporting a probable seal to dog transmission route of rabies in 2024[27].

## Towards a Case Definition for Pinniped Rabies

Two thirds of tested animals initially found alive, regardless of the clinical presentation, were rabies positive (61/94, 65%), and were either euthanised (51% of cases) or died after several hours to days (unassisted/in transit/in human care = 49%). Clinical signs of rabid seals included aggression (49%), neurological signs (48%) and being weak/unresponsive (21%). Eye-witness accounts and video media demonstrate neurological signs in rabid seals ranging from disorientation, lateral thrashing of the neck and head, muscle fasciculations in the hindquarters, nystagmus, ascending muscle weakness associated with incoordination, and dyspnoea, progressing to coma and death. Both in water and on land, rabid seals would aggressively approach and indiscriminately bite inanimate objects (e.g. surfboards, kayaks, boats, debris), conspecifics, heterospecifics (such as birds and dogs), and human water users, often triggered by auditory or visual cues from movement. At sea they displayed abnormal buoyancy and swimming behaviour such as extended circling, haphazard leaping or fighting with conspecifics. Rabid CFS were commonly encountered at the high tide mark but were reluctant to re-enter the water once ashore. When disturbed they would charge towards, rather than flee away from, the trigger (often a person or dog), in some cases barking/vocalising repeatedly, considered unusual in this generally non-territorial species.

Across age classes, non-rabid, stranded CFS were visibly emaciated, with subcutaneous fat reserves assessed during necropsy typically < 10 mm thick (all females: median = 4.0, mean = 7 mm, ± SD 8, n = 76; all males: median = 3.0, mean = 7 mm, ± SD 10 mm, n = 76, Fig. 3a). Animals with rabies often had substantive fat reserves (all females: median = 19, mean = 19 mm, ± SD 13 mm, n = 17; all males: median = 20, mean = 21 mm, ± SD 13, n = 14, Fig. 3a) and were frequently injured (n = 19/69, 38%), particularly with wounds to the head and neck, which were twice as common in rabies-positive seals (Chi-squared test 11.19, df = 1, $p = 0.0008$, n = 292).

## Rabies Incidence from Diagnostic vs. Systematic survey sampling

When combined, the results of *ad hoc* diagnostic and surveillance sampling show an incremental increase in rabies detection among CFS in South Africa between 2022 and 2025 (Fig. 2). A proactive management response, particularly effective from July 2024 onwards, to euthanise and test animals found on public beaches and displaying case definition behaviour has positively skewed the rabies incidence, which exceeds 57% for diagnostic tests (i.e., *ad hoc* sampling regime) in 2025 (Fig. 2b). Systematic carcass sampling effort, initiated to provide an unbiased assessment of seal health, increased over 2021 to 2024 but only in 2024 (22%) and 2025 (36% to October) were rabies-positive animals identified through these sampling efforts (Fig. 2b).

A generalised linear mixed effects model (GLMM) was constructed to investigate the population characteristics predictive of positive rabies cases in CFS. The best fitting model (with an $R^2$ value of 58%), presenting with good model diagnostics (Extended Results Table 1,2; Extended Fig. 4), demonstrated that animals found alive ($p < 0.0001$, GLMM) and in good or intermediate body condition ($p < 0.0001$) were more likely to be rabies positive than those emaciated or found dead when beach-cast. Age class was a significant factor in determining rabies infection (Fig. 3b), with juveniles ($p = 0.013$) and particularly adults ($p = 0.009$) more likely to have rabies than pups, but no sex bias was detected ($p = 0.41$, $p = 0.31$, Fig. 3b). Injury prevalence increased over the course of the study (Fig. 3c) in both juveniles and particularly adults; however, this was independent of rabies status. The geographic location of animal collection, grouped by closest seal colony did not account for any variance in the model (Extended Results, Table 1), however, it was retained as a random effect as it still accounts for non-independence in the data and different sampling regimes and timing.

# The Human Impact of Pinniped Rabies

Over the study period, 135 discrete incidents involving seal aggression directed towards one or more persons were documented, during which 132 individuals received Category 2 or 3 exposures [33], ranging from scratches to multiple, severe bite wounds and all warranting urgent PEP administration. These were most commonly (n = 84) acquired through commercial tourism “swim-with-seals” activities, although beach walkers, swimmers, surfers and kayakers were also attacked. In one case, the affected person was severely bitten whilst on the beach causing more than 20 puncture wounds, requiring plastic surgery including skin grafts [34]. Longer lasting psychological effects of seal attacks include insomnia and recurrent flashbacks of the incident. In four cases, immediate tracking and euthanasia of the animal was successful and rabies was confirmed in the CFS responsible. The youngest person bitten by a rabid seal was 16 years, the oldest was 78 years. Despite the opportunity for transmission and absent or incomplete PEP in cases preceding May 2024, no human cases of pinniped-contracted rabies have been recorded to date.

## DISCUSSION

Here we document the first outbreak of rabies in a marine mammal species, the Cape fur seal, with sustained maintenance of the disease in the species along the coast of South Africa since the first retrospective detection of a positive case in August 2022. On November 1st 2024, South Africa indicated to the World Organisation for Animal Health that it considered rabies to be endemic in Cape fur seals [32] and on June 14th 2025, the first rabies positive CFS was identified in central Namibia [35]. Primary considerations in the ongoing management of rabies in CFS include animal welfare, population impacts, host shift events, and spillover to humans and domesticated animals.

The outbreak of rabies in CFS has brought about several welfare concerns for both infected seals, conspecifics and other species. Systematic surveillance surveys in 2024 demonstrated that rabies was a significant factor in CFS mortality of otherwise healthy seals that year, accounting for one in five carcasses found and tested. Whereas rabies-free animals were mostly severely emaciated, indicating death from chronic illness and/or malnutrition, rabies-positive animals were typically in good to intermediate nutritional state, indicative of a relatively short interim from when the rabies infection reaches the central nervous system to death. We confirmed *in utero* infection of rabies, indicative of transplacental transmission, which is considered unusual in wildlife [30,31]. Further investigation is necessary to understand the mechanisms and incidence of this transmission route in CFS. However, the youngest viable pup with rabies was estimated two to three months old. Considering the incubation period for rabies can be as short as 6 days as recorded in human bite cases, [36] it is plausible that pups older than 6 days could have contracted the condition through an infected bite or lick rather than transplacental infection.

Infected seals are simultaneously impacted by the clinical progression of the disease, which is most severe during the 7–10 days prior to death, by injuries arising from self-inflicted destructive behaviours (i.e., repeated head banging against rocks), and by aggravated interactions with conspecifics and heterospecifics such as humans, dogs, and presumably jackals, given the strain of rabies identified in CFS. Instances of injury, dominated by facial soft tissue trauma and maxillo-mandibular fractures, increased over time regardless of rabies status, demonstrating that welfare concerns in CFS beyond the infected animals. From our behavioural observations, these likely arose from heightened and misdirected social behaviour and aggression between rabid seals and conspecifics at colonies. Similar social and physical impacts are seen in other social species, such as African Wild dogs (*Lycaon pictus*) [37].

Due to the unequal sampling effort and distances travelled by CFS, the origin of samples cannot provide an accurate reflection of the geographic distribution and true incidence of the rabies outbreak throughout the range of CFS in southern Africa. Importantly, few observations and limited sampling efforts have been conducted in Namibia and southern Angola, where approximately 60% of the species are found [38]. Animal dispersal is a significant risk factor for the perpetuation of rabies [39] and could exacerbate disease circulation in the far ranging CFS, which move unhindered by the habitat heterogeneity and the physical barriers to dispersal faced by terrestrial animals. Within this study, for example, we sampled juveniles found at Lamberts Bay and Cape Town (Simons Town) which were flipper-tagged as pups (< 4 months old) at the Kleinsee colony some ~ 300 km and ~ 600 km away, respectively (S.M.S. author data). Adult males relocated from Cape Town (Hout Bay) to Kleinsee on welfare grounds subsequently swam back to their point of origin over the course of five to seven days, a distance of some ~ 600 km (J.H.J.P and J.F. author data). Even at an $R_0$ of 1 to 2, low level circulation and occasional rabies outbreaks continue in terrestrial regions where canine rabies is endemic [40,41]. The epidemiology of rabies in CFS is undetermined, with novel host and environmental features (double layer of thick fur, thick blubber, aquatic lifestyle, diving physiology, temperature and salinity extremes), which may impose limits on disease transmission.

Left uncontrolled, this rabies outbreak may threaten the conservation status of CFS and more vulnerable marine mammal species and is especially concerning when considered in conjunction with other emerging diseases of concern such as morbillivirus and high pathogenicity H5N1 avian influenza [14,42]. For example, although Antarctic and sub-Antarctic species are considered vagrants in Africa with historically very low annual presence of individuals e.g. [43], visits appear to be increasing in frequency in South Africa and other southern continents [44,45]. Our collation of citizen science reports (2021 to present), for example, found at least 109 unique sightings of Antarctic or sub-Antarctic pinniped species throughout South Africa (southern elephant seal, *Mirounga leonia*; crabeater seal, *Lobodon carcinophagu*s; sub-Antarctic fur seal, *Arctocephalus tropicalis*; leopard seal, *Hydrurga leptonyx*). The tendency for elephant seals to haul out within or near CFS colonies, particularly during moult, provides concerning opportunities for virus spillover. However, widespread rabies control via vaccination is currently neither practical nor feasible but may be warranted in the future. Baited vaccination has proved successful in rabies control and eradication in wildlife [46] but is unsuitable for CFS and other marine mammals, which neither masticate prey nor scavenge ashore. Consequently, an experimental parenteral vaccination trial is in progress (led by authors I.J., B.G.) to assess its effectiveness on known (captive, habituated, and wild) CFS and southern elephant seals, with concurrent disease modelling efforts to assess the long-term impact of rabies on both the CFS population and other more vulnerable vagrant species along the South African coastline.

This novel host-shift event, and potential for the reintroduction of the jackal canid-rabies biotype to the domesticated dog population across the CFS distribution range, require careful consideration and new management approaches within the Global One Health framework, particularly considering the World Health Organization's (WHO) objective of zero dog-mediated rabies transmission to humans by 2030. Indeed, the transmission of pinniped rabies to a domesticated dog in Cape Town was the event that prompted the widespread testing of CFS brain samples in 2024. The vaccination history of this dog was incomplete - a single dose of the standard two dose regime in 2021, three years prior to infection, with no booster vaccinations or rabies antibody titre assessment. As 99% of global exposure to rabies in the human population is from domesticated dogs [47], wide-scale vaccination programmes for dogs are continuously implemented and enforced by law in many countries [48,49], including South Africa. However, the perception of dog immunity provided by (often incomplete) vaccinations or due to the prolonged absence of canine rabies in regions such as the Western Cape, can provide a false sense of security regarding animal protection from rabies. At least six domesticated dogs have been euthanised following exposure to rabid seals in South Africa. Consequently, in response to the outbreak, programmes of canine vaccination have been strengthened in areas where pinniped rabies has been detected, and local municipal enforcement is being considered to minimise interactions between dogs and seals.

Rabies incubation periods in human bite victims vary greatly depending on the bite location in relation to the CNS the viral load transferred, viral strain, severity of the lesion, and host species responsible for the incident [36,50,51]. Generally, the incubation periods fall between 20 and 90 days from exposure but can exceed several years [36,50,52]. In humans, PEP (rabies vaccine course plus rabies immunoglobulin) [33] is highly effective when administered as soon as possible after exposure [53]. However, until June 2024 seal bite victims were not routinely administered PEP and were vulnerable to rabies infection. Nonetheless, no case of CFS to human rabies transmission has come to light since contact tracing has been widely implemented. The enveloped RNA *Lyssavirus* virus is highly labile in the environment [54], and it is currently postulated that since many of the human victims were bitten in sea water, and often through a wetsuit, this may significantly reduce the viral load transferred. Immediate *in situ* flushing of the wound with sea water in many cases could further help to explain the current absence of human cases to date, following Category 2 and 3 bites in those who did not receive PEP or other medical intervention. However, the physical impacts of injuries inflicted through bite wounds of rabid animals can be substantial (e.g., severe wounds requiring reconstructive surgery, sepsis), and the psychological effects of potentially being infected with an incurable, fatal, disease, can be long-lasting and costly [9]. Swimmers are at an additional risk of bleeding out or drowning from in water attacks and small vessel users may suffer from exposure/hypothermia in cases where vessels/rafts are severely damaged and set adrift. Those who experienced or witnessed seal aggression reported subsequent feelings of new or increased fear in and around the coast, sufficient to significantly change their behaviour. Many among this group also earn their livelihood working as guides or naturalists, compounding the impacts of these experiences on their lives. As the virus spreads, such interactions are likely to increase, threatening public health and safety, as well as marine tourism and recreation.

Currently, the One Health approach - a holistic disease control strategy recognizing the interdependence of human, animal, wildlife and ecosystem health [55] - is widely accepted as the most effective practice to address rabies, particularly in low- and middle-income countries [56–58], which include all the countries (South Africa, Namibia, Angola) where CFS are found. Arguably, the recognition of this outbreak was delayed due to cognitive bias (ideolepsis) with no historical equivalent and confounded by an unusual mortality event simultaneously affecting seals throughout 2021–2022. However, since June 2024 there has been a significant multiple stakeholder response focused on detection, public awareness and PEP. Considering the Global Strategic Plan of zero dog-mediated deaths from rabies by 2030 [59], this outbreak must be a lesson in the need for vigilance in non-host species. It should also stimulate interest in developing disease prevention methods in free roaming marine and terrestrial mammalian species.

# METHODS

A broad investigation into seal health was initiated in 2021, following several unusual mortality events (UMEs) of CFS along the west coast of South Africa (2021) and Namibia (2020, 2021) (authors' unpublished data). Several differential diagnoses (malnutrition, avian influenza, morbillivirus, domoic acid/DA toxicosis) were considered specific to the 2021 UME in South Africa, but no single causative pathogen was identified. Similarities in the ecology and life-history of CFS to California sea lions (*Zalophus californianus*), which are frequently affected by DA toxicosis [60], uplisted biotoxin exposure as a strong candidate for differential diagnosis in the CFS UME. Consequently, a research study for DA toxicosis in CFS was initiated by the authors, which included full brain extraction and storage in 10% buffered formalin within the standard operating procedures. This study evolved to include rabies virus detection following routine histopathologic examination of central nervous tissue to detect possible DA exposure; the rabies focus was fast tracked by increased documentation of rabies-like behaviour in CFS, and suspected seal to domestic dog transmission.

Carcass sampling was conducted in South Africa between 2021–2025, with the geographic extent of data collection covering ~ 1,000 km of South African coastline, encompassing multiple established breeding colonies (Kleinsee, Lamberts Bay, Vondeling Island, Dassen Island, Duiker Island, False Bay Seal Island, Dyer Island, Mossel Bay Seal Island, Robberg Peninsula and Black Rocks), which for island colonies included the adjacent coastline (Fig. 1). Carcass sampling efforts reflected availability of and access to, fresh carcasses, as well as the presence of wildlife response teams and citizen scientist reporting efforts. Sampling of fresh carcasses included both those found ashore (i.e., no case history, beach-cast) or sick/moribund animals found alive (i.e., with clinical case history). When found alive, seals may have subsequently died unaided *in situ*, or during transport or rehabilitation efforts. Alternatively, following poor prognosis of survival due to injury/body condition or observed pathology, animals were humanely euthanised.

For fresh carcasses i.e., Class 2, [61] where possible a comprehensive and standard set of organ tissue samples (brain, heart, lung, liver, spleen, pancreas, kidney, lymph node, and adrenal gland) were collected in duplicate along with auxiliary information including gross observations, age, sex, standard body length (SL) from snout to tail tip, subcutaneous fat/blubber depth (mm) and a complete set of high resolution photographs. One sample set was stored frozen at -20 °C (or, in the case of brain material, in glycerol saline solution) and another fixed in 10% buffered formalin. Where carcass removal was not possible, due to logistical constraints or advanced decomposition Class 3 of 4, [61], a reduced set of biological samples and metadata were collected. Occasionally, a brain section (or the whole head) was stored frozen at -20 °C for molecular investigation for pathogens on a case-by-case basis.

Since confirmation of rabies in May 2024, and the associated increased biosafety risk, brain sampling methods in favour of decreased biosafety risk were employed. The “straw” sampling approach was preferred over full brain removal. Modification of sampling methods depended on carcass decomposition, sampling team and site. Collection included the “straw” sampling method [62] with modification using a metal straw for increased durability and, where necessary, increasing sample volume using a tongue depressor to remove cerebellum and brainstem tissue through the foramen magnum. For advanced scavenged carcasses, access to the brain could be achieved through the optic nerve foramen in the skull. In these cases, brain samples were taken by passing a straw through the optic nerve foramen directed to or through the foramen magnum. Where available, observational videos collected from hours to days prior to death were collated and reviewed to help characterise terminal disease presentation and progression in live CFS. Together with eyewitness reports and expert opinions, these were used to develop a working clinical case definition of rabies in CFS. When necropsy metadata were absent (i.e., in cases where carcass sampling was conducted by third parties), photo/video media were used to assess general body condition (emaciated, intermediate, healthy) and injury presence.

# Rabies testing of brain material

Rabies was confirmed from brain samples through dFAT and/or IMP, depending on sample storage and availability. The fundamental principle of the Fluorescent Antibody Test depends upon the microscopic detection of viral antigens using Fluorescein isothiocyanate (FITC)-Conjugated antibodies to RABV. Testing followed standard protocols[63] as summarised here: Touch slide impressions of CNS tissue (brain stem, cerebellum, hippocampus), were prepared and fixed with chilled (-20 °C) acetone for at least 15 minutes and air dried for 5 minutes. Each slide was stained with 80 ul of fluorescein isothiocyanate (FITC) labelled polyclonal antibody conjugate (Bio-Rad, California, USA) and incubated at 37 °C for 30 minutes. Thereafter, the slides were washed twice with phosphate buffered saline (PBS, 0.1 M, pH 7.2–7.4) and counter-stained with 0,00125% Evans Blue solution (Merck, Germany). The slides were examined using a fluorescence microscope at 200x magnification (Zeiss, Germany) and the fluorescence intensity and antigen distribution was rated between one and four (i.e. one referring to less distribution and four abundant distribution).

Immunohistochemistry (IHC) uses the principle of antigen-antibody reaction to identify specific antigens [63]. IHC was used to identify RABV in brain material collected prior to June 2024 that was fixed in 10% neural buffered formalin and paraffin fixed as 4-μm thick sections. The presence of RABV was assessed using IMP processing and labelling following a validated method as described by Claassen et al. [27]. In brief: this method involves blocking endogenous peroxidases with 3% hydrogen peroxide, microwave retrieval in Tris-EDTA buffer (pH9) for 21 minutes and then incubation with the anti-RABV primary antibody at a 1:500 dilution for 1 hour. We used a primary polyclonal rabbit anti-lyssavirus ribonucleoprotein antibody (Ministry of Agriculture, Food and Rural Affairs, Agricultural Research Institute of Ontario, Canada, lot 9/2/88) for this test. Slide evaluation was performed using a standard light microscope whereby low-grade labelling was defined as positive labelling present in the neuroparenchyma in < 10% of the slides examined, intermediate-grade labelling was defined as 10–25% positive labelling and high-grade labelling was defined as > 25% positive labelling [27].

# Human Impact of Pinniped Rabies

Concurrent to the initial DA research study, several informal qualitative interviews were conducted with coastal guides/naturalists who had experienced or witnessed unusual or “new” seal behaviour. Questions centred on detailed descriptions of the seals’ behaviour and the personal after-effects for the interviewee, and responses were analysed for common themes. Data streams used to quantify incidents of suspect or confirmed rabid seals were diverse, but included a 70 + member stakeholder reporting network, review of online and printed media reports, rabies reporting through the national centre of infectious diseases and personal communications with one or more authors. Reports were verified through direct contact with the affected parties with written requests for data sharing to a standard online questionnaire and case folder.

# Statistical Analysis

A binomial generalised linear mixed modelling (GLMM) approach, with a logit link function, using the package 'lme4' [64] in 'R' statistical software version 4.1.3 [65] was used to investigate the key characteristics of rabies-positive CFS. Here, the rabies status of all animals tested where metadata were available (n = 267, positive or negative regardless of testing method) was modelled as a function of the following categorical fixed effects: age class (adult/subadult, juvenile, pup), sex (male, female, unknown), body injury (present, absent), body condition (emaciated, intermediate, healthy), whether initially found alive or not (alive, dead), and survey type (ad hoc sampling, survey). The location of each seal was included as a categorical random effect, whereby the South African coastline was divided into sites according to the proximity to nearest CFS breeding colony (Fig. 2). Due to sample size restrictions, only eight of the ten colonies were included in the model (Dyer Island and Black Rocks excluded, n = 4 for each colony). The models were fitted in a stepwise fashion, using the Akaike Information Criterion (AIC) to select the best-fitting model. Model performance was then assessed through overall fit using the quantile-quantile (Q-Q) residuals plot, Kolmogorov–Smirnov (KS) test for normality, over- and under-dispersion test, and zero-inflation test using the 'DHARMa' R package [66], and the conditional and marginal $R^2$ values were calculated using the R package 'MuMIn' [67].

# Declarations

### PERMITS & ETHICS

Research data were collected in terms of research permits issued to authors (TG RES 2021/97, 2022/81, RES2024/41, RES2025-88, CN44-87-16854, CN43-29-21036, GH RES2023/51, RES2024/57, RES2025/87, IJ RES2024-22) and animal ethics (TG University of Stellenbosch institutional review board ACU-2021-15015, ACU-2024-30229, IJ T2601/94) or human ethics (AD REB File #: 22-01-028) approvals from their relevant academic institutions. We confirm that the South African Department of Animal Health provided no objection to the publishing of this work.

### AUTHOR STATEMENTS

The authors declare no competing interests.

Supplementary Information is available for this paper.

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### AUTHOR CONTRIBUTION

**T.G., N.K., L.P.M., J.C.A.S., G.H., S.H.E., R.P.:** Contributed to conception, project administration, data collection, logistical support, data analysis, drafting and figures. **G.F.:** Contributed to conception, data collection and logistical support. **I.J., G.S., G.O., A.D., A.B., S.D., C.N., A.C., J.F., J.H.J.P., S.M.S.:** Contributed to data collection, logistical support and drafting. **B.G., L.B.:** Contributed to conception, logistical support and drafting.

# DATA AVAILABILITY

The datasets on seal health generated and analysed during the current study are available from the corresponding author on reasonable request.

# INFORMED CONSENT STATEMENT

Written consent to use the images in Fig. 1 for this scientific publication was provided to the author TG in October 2025. Written consent to include summary details and images (Fig. 4) of injuries resulting from seal interactions was provided by participants on varying dates between 2024-2025 according to the declaration of Helsinki, and all participants are anonymised.

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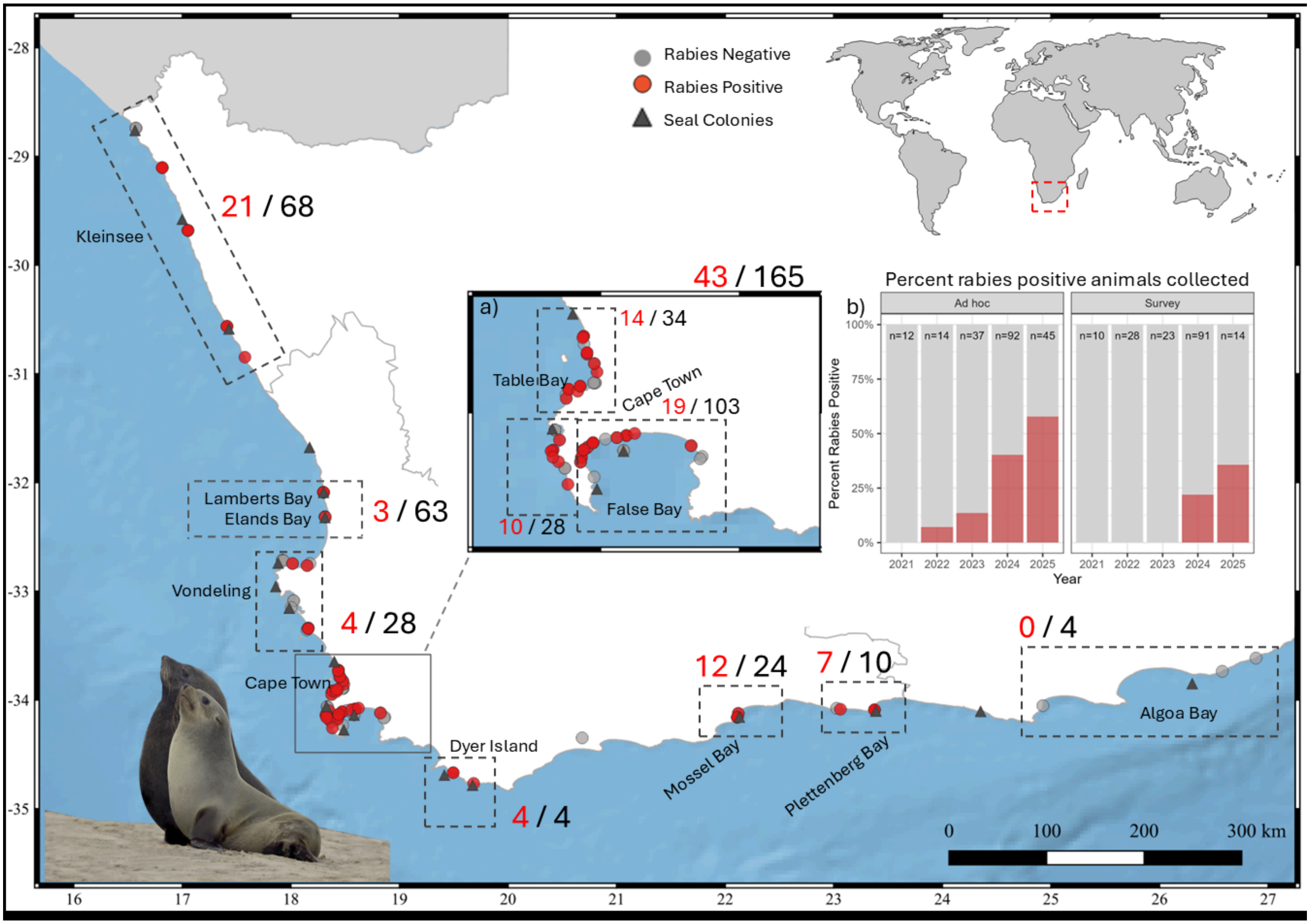
# Figures

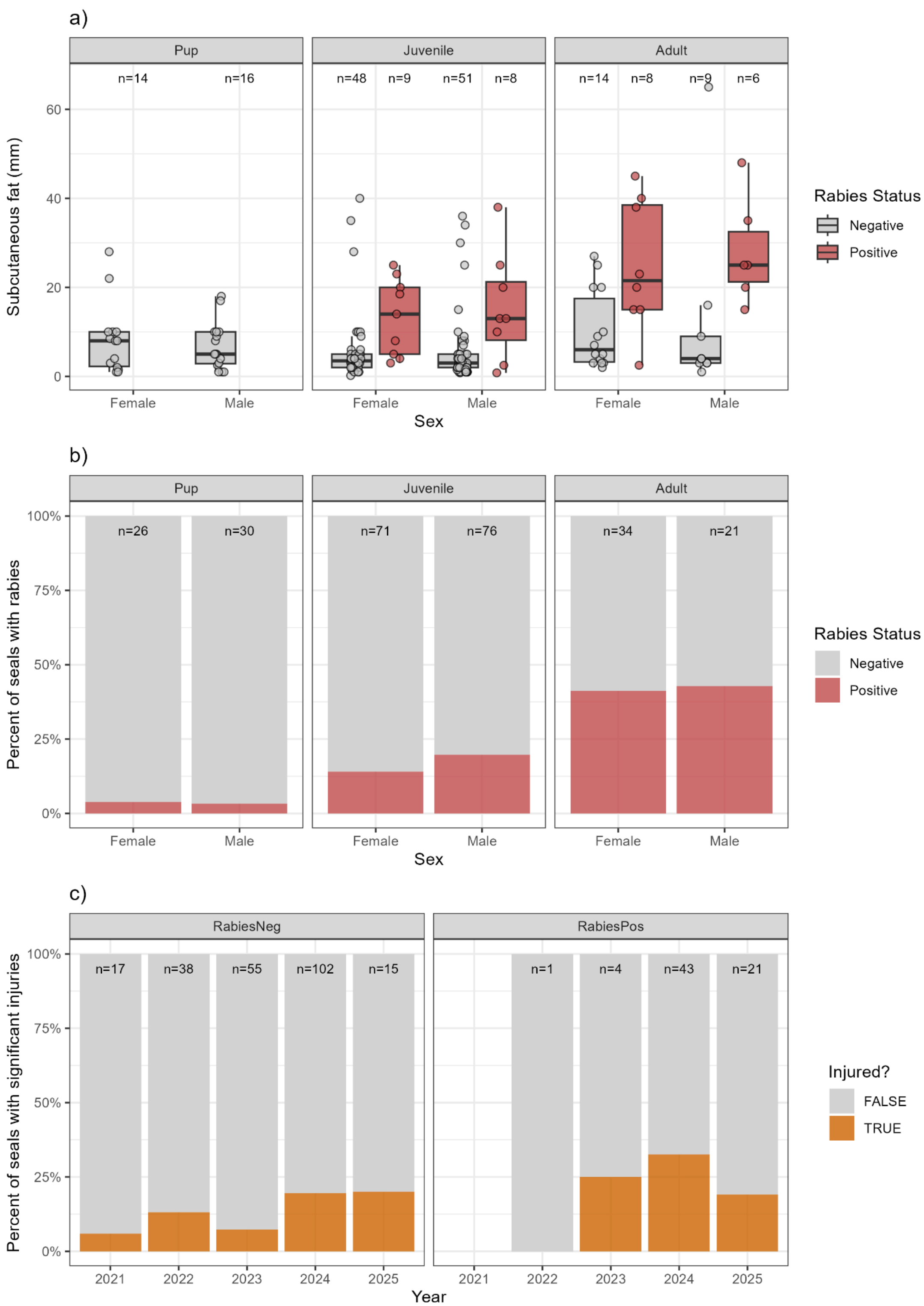

### Figure 1

**Clinical examination of Cape fur seal carcasses. a)** A subadult male from Big Bay, Cape Town, was the first animal to test rabies positive through dFAT. The animal exhibited aggression and had traumatic puncture wounds to the head. **b)** Severe, traumatic facial injuries to an adult female CFS stranded alive on Kommetjie Beach, Cape Town in May 2020. The animal was caught and immediately euthanised. Inspection of facial wounds indicated likely infliction of injuries by a conspecific. IMP testing was rabies negative. **c)** Adult female with rabies recovered from Stony Point Nature Reserve showing severe injuries to the lower jaw. **d)** Rabies positive CFS foetus recovered from a rabies positive female CFS euthanised in Mossel Bay after showing clinical signs of rabies.




## Figure 2

**Map of South Africa showing the location of Cape fur seals tested for rabies and the number of rabies-positive seals between 2021 and 2025. Insert a)** Close up of the sampling effort in Cape Town and surrounding area. **Insert b)** Proportion (expressed as the percentage) of Cape fur seals with rabies between 2021 - 2025, relative to sampling regime (*ad hoc*/diagnostic sampling vs. systematic carcass survey). Sample sizes used to generate proportions are shown to the top of each column.




## Figure 3

**Summary plots of rabies in Cape fur seals. a)** Subcutaneous fat (mm) quantification measured in necropsied seals (one measurement per animal taken from the dorsal midline) relative to rabies status and split by age class. Displayed as boxplots with median and inter-quartile ranges, with raw data values jittered as overlapping points, and sample sizes indicated to the top of each panel. In most cases, rabies-negative animals are emaciated, with similar subcutaneous fat reserves across age/sex, indicative of chronic illness and/or malnutrition. Those with rabies are often in a good nutritional state, indicative of a short duration of ill health. **b)** Proportion (%) of Cape fur seals with rabies demonstrating an overall increase in incidence across age classes but little difference between males and females. **c)** Proportion (%) of adult and juvenile Cape fur seals with injuries over time. Sample sizes used to generate proportions are shown to the top of each column.


**Figure 4**

Examples of the nature and severity of injury suffered by coastal water users by Cape fur seals with confirmed or suspect rabies. (a) Injury to the calf sustained through attack by a seal during a “swim with seals” experience in Cape Town 2024, b) Bite to the hand sustained during an aggressive interaction between a domestic dog and seal on a Cape Town beach 2024, c) Bite wound to the foot, requiring 16 stitches sustained during “swim with seals” experience in Plettenberg Bay 2025, d) Damage to property (surf board) sustained during attack by a rabid seal on Muizenberg Beach, Cape Town in May 2024, e) Damage to wetsuit sustained during a seal attack on a snorkeler near a seal colony.

## Supplementary Files

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- EXTENDEDRESULTS.docx