Rabies as a threat to wildlife

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Summary

The impact of infectious disease may become progressively more harmful to a species' survival as a wild population approaches an 'extinction vortex'. This risk is especially relevant for pathogens that spread rapidly and result in high mortality rates. Rabies, a virus that infects many mammalian species, can be efficiently transmitted through infected saliva, and is fatal without prior vaccination or rapid post-exposure prophylaxis (in humans). The authors conducted an extensive literature review to identify all wild mammal species reported to have been infected with rabies virus. They found reports of infection in 190 mammalian species, including 16 with elevated risk of extinction and two for which rabies is a direct conservation threat: the Ethiopian wolf (*Canis simensis*) and the African wild dog (*Lycaon pictus*). This paper discusses selected examples in which rabies has contributed to the population decline of a species of conservation concern. In addition, the authors note the importance of the transmission of rabies virus (RABV) from domestic dogs to wildlife, and the many challenges associated with the vaccination of wild animals. With this in mind, they present potential solutions to reduce the burden of rabies on wildlife. Once stable control of RABV is achieved in domestic dogs, remaining rabies threats to wildlife conservation can be addressed more effectively.

Keywords

Biodiversity – Conservation – Domestic dog – Extinction – One Health – Rabies – Vaccination – Wildlife.

Introduction

Mortality associated with infectious disease is increasingly being recognised as a major threat to the survival of wild animal species. Emerging infectious diseases, either arising *de novo* in a species or introduced to a region or population that lacks immunity, have led to severe die-offs of wild animals in recent decades, presenting concerns for biodiversity conservation (1, 2). Infectious diseases can also serve important ecological functions, such as regulating population size and food webs. However, human activities are changing the ecological dynamics of infectious disease transmission and facilitating the global movement of pathogens. As a consequence, the distribution, abundance and population structure of wildlife species are changing, and the encroachment of invasive or domestic species into wild animal habitats creates new opportunities for pathogen transmission.

When species exist as resilient populations and meta-populations, infectious disease outbreaks may not present serious risks to species survival. Such populations can experience declines but rebound efficiently or be recolonised by individuals from adjacent populations. However, for species that already face extinction from various pressures,

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infectious disease can be a significant additional factor in the 'extinction vortex' (3). In line with the Allee effect, populations controlled by density-dependent factors, and which are already reduced in size, may be at increased risk of extinction from disease-associated declines (4).

Rabies

The burden of rabies virus (RABV) on human and domestic animal health has been well established. Tens of thousands of human deaths per year are attributed to RABV infections acquired from domestic dogs (*Canis familiaris*) (5, 6). There are also recognised disease effects on domestic dogs, and associated welfare concerns related to dog control strategies (7). However, beyond the role of certain wild animals as sylvatic reservoirs of RABV, limited attention has been paid to the possible negative impact of rabies on wildlife populations, despite its broad host range and known impact on a few threatened species.

There are many variants of RABV. All such variants can cause fatal disease in humans and in domestic and wild mammals, with perhaps a few exceptions, which remain to be clarified (8, 9). However, there are complex relationships among RABV variants and mammalian host species, which affect virus persistence, transmission, and disease occurrence over a wide range of ecological settings (10, 11). On most continents, domestic dogs are the principal reservoir and source of infection for canine RABV, which is transmitted to a wide range of species (12). To more fully assess the potential impact of RABV on mammalian species at risk, the authors conducted an extensive literature review to identify all species in which RABV has been detected. The conservation status of each known host species was then determined, and the two data sets and ecological information were considered together to provide an overview of the potential effects of RABV on populations of host species.

Methods

The authors searched the peer-reviewed literature from 1940–2015, using the search term 'rabies', on Web of Science, PubMed and Google Scholar. In addition, they searched books, reviews, and literature cited in references that the authors had obtained by using a database assembled for mammalian host–virus relationships (13). Host species reported in the *Compendium of the OIE Global Conference on Rabies Control* were also included if the information could be traced back to an original report (14). The authors included additional virus–host associations from the Global Mammal Parasite Database for primate, carnivore and ungulate viruses, as of November 2006 (12), and other published reviews specific to bats and rodents (15, 16, 17) that were not included in the original peer-reviewed literature searches.

The authors' database was not exhaustive and did not include all references for a given host–rabies association, as only one reference per association was selected, with a preference for detection methods that included virus isolation or polymerase chain reaction (PCR) with sequencing. The authors only included associations via antibody or antigen detection if virus isolation or molecular methods could not be identified by searching for reports of RABV infection of that host species in the extensive literature. The authors excluded papers published in languages other than English, all records without species-level host information, and those for which the authors could not track down the primary reference(s). Records of mammalian RABV infections from experimental studies, infections in zoo animals and cell cultures were also excluded. Rabies-infected species reported to the World Animal Health Information System (WAHIS) of the World Organisation for Animal Health (OIE) from Member and non-Member Countries were included for the years 2012–2014 (18). Prior WAHIS records were not used because they do not include the name of the host species.

The conservation status of each host species was taken from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, Version 2014.3 (19). To interpret their findings, the authors conducted descriptive statistical analyses and reviewed additional literature via targeted searches (e.g. 'affected species' and 'rabies') for evidence of the direct effects of RABV on animal populations and biodiversity.

Results

Rabies virus infection was reported in 190 mammalian species (Tables I and II). The majority of these species (95%) meet the OIE and Food and Agriculture Organization of the United Nations (FAO) definitions of 'wild animals': an animal that has a phenotype unaffected by human selection and lives independent of direct human supervision or control (31) (Table II).

Methods used to detect RABV infection included PCR or virus isolation (51% of reported species), and antigen or antibody detection (22%). In 27% of reports, the method used was not specified. Species from the taxonomic order Chiroptera comprised 46% of the reported species, followed by Carnivora (33%) and Rodentia (8%) (Table II).

Observed infected species as a proportion of the total number of species per order ranged from 0.2% (order Eulipotyphla) up to 50% (order Proboscidea) (Table I). Seven of the

Table I
Mammalian orders in which infection with rabies virus has been reported

Order	Infected species	Total no. in order	% of order
Chiroptera	88	1,150	7.7
Carnivora	62	287	21.6
Rodentia	16	2,258	0.7
Cetartiodactyla	12	329	3.7
Primates	6	430	1.4
Perissodactyla	2	16	12.5
Hyracoidea	1	5	20.0
Lagomorpha	1	93	1.1
Proboscidea	1	2	50.0
Eulipotyphla	1	450	0.2
Total	**190**	**5,020**	

infected species were categorised as 'Endangered', five as 'Vulnerable' and four as 'Near Threatened'. Of these species with elevated extinction risk, those from the taxonomic order Carnivora comprised 56%, followed by Chiroptera (25%), Primates (13%) and Proboscidea (6%). Overall, 8% of infected species were in a category of conservation concern; the others were classified as 'Least Concern', 'Data Deficient' or 'Not Evaluated' (Table III).

Discussion

The results of this review are consistent with the broad mammalian host range for RABV in previous reports (10, 25, 32). However, current knowledge of the host range of RABV is clearly incomplete. The 190 affected host species found in this review constitute only 4% of the known species of mammals worldwide, despite the fact that, in principle at least, all mammals are susceptible to rabies. Additionally, the authors found reports of RABV infection in fewer than 2% of the Lagomorpha and Primates species, only 0.7% of Rodentia species, and 0.2% of Eulipotyphla species (Table I). This likely represents either a surveillance bias or a consequence of transmission route. Most of the world's rodent species are unexamined for RABV infection to date, and those that are bitten by RABV-infected hosts may be unlikely to survive long enough to develop the disease (such as small rodents predated by carnivores).

The IUCN Red List classifications of species' conservation status estimate the global status of a species and thus, in some cases, may not capture severe local risks of endangerment or extinction (33). In addition, outbreaks in a given species may also have wider ecosystem impacts. Such outbreaks may alter food webs, thereby indirectly affecting already threatened species, as demonstrated in a 1982 outbreak of rabies in Namibian greater kudu (*Tragelaphus strepsiceros*) that resulted in diminished wild food sources for cheetah (*Acinonyx jubatus*) populations (34). This led to increased cheetah predation of livestock, spurring retribution killings of cheetahs by farmers (35).

To the knowledge of the authors, this review represents the most complete compilation of species observed to have been infected by RABV that is available. However, lack of surveillance or deficient reporting efforts may account for the potential lack of detection of RABV infection in species from regions where the risk of infection is high. An example can be seen in the detection of RABV in retrospective testing of ferret badgers (*Melogale moschata*) in Chinese Taipei, previously believed to have been rabies free for more than 50 years (36). Furthermore, the IUCN is continually updated. Therefore, levels of conservation concern could vary slightly with newer assessments of the status of populations.

The authors' criteria for determining rabies-infected hosts included all strains and multiple detection methods. The authors realise that there may be cross-reactivity from other lyssaviruses, which may serve as a confounding factor, and would potentially show an increased number of observed hosts in these results. Moreover, those species for which only seropositivity was reported may not represent true infection. Not all reports in the literature include the serotype, and the level of reporting varies. The authors did not, therefore, include serotype information in their results.

Impact of rabies virus on wild animals of conservation concern

This review demonstrates that RABV has affected mammalian species at an elevated extinction risk from multiple taxonomic orders (Carnivora, Chiroptera, Primates and Proboscidea). For certain species, such as the African wild dog (*Lycaon pictus*) and Ethiopian wolf (*Canis simensis*), RABV outbreaks have led directly to severe decreases in population size and local endangerment or extinction. For other species of conservational concern, occasional rabies cases may contribute to overall population declines in conjunction with other pressures, such as habitat fragmentation, decreased food availability and illegal killing. Both endemic strains of domestic dog RABV and sylvatic RABV strains have been implicated in the infection of many of these taxa, which is important information in terms of conservation and control.

Of the affected carnivores with an elevated extinction risk, African wild dog (*L. pictus*) and Ethiopian wolf (*C. simensis*) populations have experienced the most severe declines as a consequence of repeated exposure to and intra-population transmission of RABV (37, 38).

Table II
Host species in which infection with rabies virus was reported, based on peer-reviewed literature and reports to the World Organisation for Animal Health (OIE) World Animal Health Information System (WAHIS)
See (13) for all original records collated into a database by Olival *et al.* and referenced here as (13)

	Reported host species	Order	Family	Wild or domestic status	IUCN Red List status	Detection method*	Reporting source
1	*Acinonyx jubatus*	Carnivora	Felidae	Wild	VU	0	(20)
2	*Alces alces*	Cetartiodactyla	Cervidae	Wild	LC	NA	(18)
3	*Alopex lagopus*	Carnivora	Canidae	Wild	LC	1	(13)
4	*Antrozous pallidus*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
5	*Artibeus cinereus*	Chiroptera	Phyllostomidae	Wild	LC	0	(12)
6	*Artibeus fimbriatus*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
7	*Artibeus jamaicensis*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
8	*Artibeus lituratus*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
9	*Artibeus phaeotis*	Chiroptera	Phyllostomidae	Wild	LC	0	(22)
10	*Artibeus planirostris*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
11	*Atilax paludinosus*	Carnivora	Herpestidae	Wild	LC	1	(23)
12	*Bos taurus*	Cetartiodactyla	Bovidae	Domestic	NE	0	(13)
13	*Callithrix jacchus*	Primates	Cebidae	Wild	LC	NA	(18)
14	*Camelus dromedarius*	Cetartiodactyla	Camelidae	Domestic	NE	1	(24); camel species inferred from region
15	*Canis adustus*	Carnivora	Canidae	Wild	LC	NA	(13)
16	*Canis aureus*	Carnivora	Canidae	Wild	LC	0	(18)
17	*Canis familiaris*	Carnivora	Canidae	Domestic	NE	1	(25)
18	*Canis latrans*	Carnivora	Canidae	Wild	LC	1	(13)
19	*Canis lupus*	Carnivora	Canidae	Wild	LC	1	(13)
20	*Canis mesomelas*	Carnivora	Canidae	Wild	LC	1	(13)
21	*Canis simensis*	Carnivora	Canidae	Wild	EN	1	(13)
22	*Capra hircus*	Cetartiodactyla	Bovidae	Domestic	NE	1	(13)
23	*Capreolus capreolus*	Cetartiodactyla	Cervidae	Wild	LC	NA	(18)
24	*Caracal caracal*	Carnivora	Felidae	Wild	LC	NA	(18)
25	*Carollia perspicillata*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
26	*Castor fiber*	Rodentia	Castoridae	Wild	LC	NA	(18)
27	*Cerdocyon thous*	Carnivora	Canidae	Wild	LC	NA	(18)
28	*Chrysocyon brachyurus*	Carnivora	Canidae	Wild	NT	0	(26)
29	*Civettictis civetta*	Carnivora	Viverridae	Wild	LC	NA	(18)
30	*Corynorhinus townsendii*	Chiroptera	Vespertilionidae	Wild	LC	1	(13, 27)
31	*Crocuta crocuta*	Carnivora	Hyaenidae	Wild	LC	1	(25)
32	*Cuon alpinus*	Carnivora	Canidae	Wild	EN	NA	(18)
33	*Cynictis penicillata*	Carnivora	Herpestidae	Wild	LC	1	(28)
34	*Cynomops abrasus*	Chiroptera	Molossidae	Wild	DD	1	(13)
35	*Cynomops planirostris*	Chiroptera	Molossidae	Wild	LC	NA	(13)
36	*Cynopterus brachyotis*	Chiroptera	Pteropodidae	Wild	LC	1	(13)
37	*Desmodus rotundus*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
38	*Diaemus youngi*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
39	*Diclidurus albus*	Chiroptera	Emballonuridae	Wild	LC	1	(13)

Table II (cont.)

	Reported host species	Order	Family	Wild or domestic status	IUCN Red List status	Detection method*	Reporting source
40	*Diphylla ecaudata*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
41	*Elephas maximus*	Proboscidea	Elephantidae	Wild	EN	1	(29)
42	*Eptesicus brasiliensis*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
43	*Eptesicus diminutus*	Chiroptera	Vespertilionidae	Wild	DD	1	(13)
44	*Eptesicus furinalis*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
45	*Eptesicus fuscus*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
46	*Eptesicus serotinus*	Chiroptera	Vespertilionidae	Wild	LC	1	(18)
47	*Eptesicus somalicus*	Chiroptera	Vespertilionidae	Wild	LC	NA	(18)
48	*Equus asinus*	Perissodactyla	Equidae	Domestic	NE	0	(13)
49	*Equus caballus*	Perissodactyla	Equidae	Domestic	NE	0	(13)
50	*Erethizon dorsatum*	Rodentia	Erethizontidae	Wild	LC	0	(13)
51	*Euderma maculatum*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
52	*Eumops auripendulus*	Chiroptera	Molossidae	Wild	LC	1	(13)
53	*Eumops glaucinus*	Chiroptera	Molossidae	Wild	LC	1	(13)
54	*Eumops patagonicus*	Chiroptera	Molossidae	Wild	LC	1	(13)
55	*Eumops perotis*	Chiroptera	Molossidae	Wild	LC	1	(13)
56	*Felis catus*	Carnivora	Felidae	Domestic	NE	1	(13)
57	*Felis lybica*	Carnivora	Felidae	Wild	NE	NA	(18)
58	*Felis manul*	Carnivora	Felidae	Wild	NE	NA	(18)
59	*Felis nigripes*	Carnivora	Felidae	Wild	VU	1	(23)
60	*Felis silvestris*	Carnivora	Felidae	Wild	LC	1	(25)
61	*Galerella sanguinea*	Carnivora	Herpestidae	Wild	LC	NA	(18)
62	*Genetta genetta*	Carnivora	Viverridae	Wild	LC	1	(25)
63	*Giraffa camelopardalis*	Cetartiodactyla	Giraffidae	Wild	LC	NA	(18)
64	*Glaucomys volans*	Rodentia	Sciuridae	Wild	LC	0	(25)
65	*Glossophaga longirostris*	Chiroptera	Phyllostomidae	Wild	DD	0	(13)
66	*Glossophaga morenoi*	Chiroptera	Phyllostomidae	Wild	LC	0	(22)
67	*Glossophaga soricina*	Chiroptera	Phyllostomidae	Wild	LC	0	(13)
68	*Herpestes ichneumon*	Carnivora	Herpestidae	Wild	LC	NA	(18)
69	*Herpestes javanicus*	Carnivora	Herpestidae	Wild	LC	NA	(18)
70	*Herpestes sanguineus*	Carnivora	Herpestidae	Wild	LC	1	(23)
71	*Histiotus macrotus*	Chiroptera	Vespertilionidae	Wild	LC	NA	(18)
72	*Histiotus montanus*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
73	*Histiotus velatus*	Chiroptera	Vespertilionidae	Wild	DD	0	(13)
74	*Homo sapiens*	Primates	Hominidae	Human	LC	1	(13)
75	*Hyaena hyaena*	Carnivora	Hyaenidae	Wild	NT	NA	(18)
76	*Hydrochoerus hydrochaeris*	Rodentia	Caviidae	Wild	LC	1	(13)
77	*Hylobates lar*	Primates	Hylobatidae	Wild	EN	NA	(18)
78	*Ichneumia albicauda*	Carnivora	Herpestidae	Wild	LC	1	(25)
79	*Ictonyx striatus*	Carnivora	Mustelidae	Wild	LC	NA	(18)
80	*Lasionycteris noctivagans*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
81	*Lasiurus blossevillii*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)

Table II (cont.)

	Reported host species	Order	Family	Wild or domestic status	IUCN Red List status	Detection method*	Reporting source
82	*Lasiurus borealis*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
83	*Lasiurus cinereus*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
84	*Lasiurus ega*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
85	*Lasiurus egregius*	Chiroptera	Vespertilionidae	Wild	DD	NA	(13)
86	*Lasiurus intermedius*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
87	*Lasiurus seminolus*	Chiroptera	Vespertilionidae	Wild	LC	1	(13, 27)
88	*Lasiurus xanthinus*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
89	*Leptonycteris curasoae*	Chiroptera	Phyllostomidae	Wild	VU	0	(22)
90	*Leptonycteris nivalis*	Chiroptera	Phyllostomidae	Wild	EN	1	(27)
91	*Lepus europaeus*	Lagomorpha	Leporidae	Wild	LC	NA	(18)
92	*Lontra canadensis*	Carnivora	Mustelidae	Wild	LC	0	(13)
93	*Lycalopex griseus*	Carnivora	Canidae	Wild	LC	NA	(18)
94	*Lycaon pictus*	Carnivora	Canidae	Wild	EN	1	(25)
95	*Lynx lynx*	Carnivora	Felidae	Wild	LC	NA	(18)
96	*Lynx rufus*	Carnivora	Felidae	Wild	LC	0	(13)
97	*Macrotus californicus*	Chiroptera	Phyllostomidae	Wild	LC	1	(27)
98	*Marmota monax*	Rodentia	Sciuridae	Wild	LC	1	(13)
99	*Martes foina*	Carnivora	Mustelidae	Wild	LC	NA	(18)
100	*Martes martes*	Carnivora	Mustelidae	Wild	LC	1	(18)
101	*Martes pennanti*	Carnivora	Mustelidae	Wild	LC	0	(13)
102	*Meles leucurus*	Carnivora	Mustelidae	Wild	LC	NA	(18)
103	*Meles meles*	Carnivora	Mustelidae	Wild	LC	NA	(18)
104	*Mellivora capensis*	Carnivora	Mustelidae	Wild	LC	NA	(13)
105	*Melogale moschata*	Carnivora	Mustelidae	Wild	LC	NA	(18)
106	*Mephitis mephitis*	Carnivora	Mephitidae	Wild	LC	1	(13)
107	*Micronycteris megalotis*	Chiroptera	Phyllostomidae	Wild	LC	0	(22)
108	*Molossops neglectus*	Chiroptera	Molossidae	Wild	DD	0	(13)
109	*Molossus molossus*	Chiroptera	Molossidae	Wild	LC	1	(13)
110	*Molossus rufus*	Chiroptera	Molossidae	Wild	LC	1	(13)
111	*Mormoops megalophylla*	Chiroptera	Mormoopidae	Wild	LC	0	(13)
112	*Mungos mungo*	Carnivora	Herpestidae	Wild	LC	NA	(18)
113	*Mus musculus*	Rodentia	Muridae	Wild	LC	0	(21)
114	*Mustela putorius*	Carnivora	Mustelidae	Wild	LC	NA	(18)
115	*Myocastor coypus*	Rodentia	Myocastoridae	Wild	LC	0	(21)
116	*Myotis albescens*	Chiroptera	Vespertilionidae	Wild	LC	0	(13)
117	*Myotis austroriparius*	Chiroptera	Vespertilionidae	Wild	LC	0	(27)
118	*Myotis californicus*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
119	*Myotis chiloensis*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
120	*Myotis daubentoni*	Chiroptera	Vespertilionidae	Wild	NE	NA	(18)
121	*Myotis evotis*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
122	*Myotis grisescens*	Chiroptera	Vespertilionidae	Wild	NT	1	(21)
123	*Myotis keenii*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)

Table II (cont.)

	Reported host species	Order	Family	Wild or domestic status	IUCN Red List status	Detection method*	Reporting source
124	*Myotis leibii*	Chiroptera	Vespertilionidae	Wild	LC	1	(27)
125	*Myotis levis*	Chiroptera	Vespertilionidae	Wild	LC	NA	(13)
126	*Myotis lucifugus*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
127	*Myotis nattereri*	Chiroptera	Vespertilionidae	Wild	LC	NA	(18)
128	*Myotis nigricans*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
129	*Myotis riparius*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
130	*Myotis septentrionalis*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
131	*Myotis thysanodes*	Chiroptera	Vespertilionidae	Wild	LC	0	(27)
132	*Myotis velifer*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
133	*Myotis volans*	Chiroptera	Vespertilionidae	Wild	LC	0	(30)
134	*Myotis yumanensis*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
135	*Nasua nasua*	Carnivora	Procyonidae	Wild	LC	NA	(18)
136	*Neotoma floridana*	Rodentia	Cricetidae	Wild	LC	0	(13)
137	*Nyctalus noctula*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
138	*Nyctereutes procyonoides*	Carnivora	Canidae	Wild	LC	1	(13)
139	*Nycticeius humeralis*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
140	*Nyctinomops laticaudatus*	Chiroptera	Molossidae	Wild	LC	1	(13)
141	*Nyctinomops macrotis*	Chiroptera	Molossidae	Wild	LC	1	(13)
142	*Ondatra zibethicus*	Rodentia	Cricetidae	Wild	LC	NA	(18)
143	*Oryx gazella*	Cetartiodactyla	Bovidae	Wild	LC	NA	(18)
144	*Otocyon megalotis*	Carnivora	Canidae	Wild	LC	1	(25)
145	*Ovis aries*	Cetartiodactyla	Bovidae	Domestic	NE	0	(25)
146	*Panthera leo*	Carnivora	Felidae	Wild	VU	NA	(18)
147	*Panthera pardus*	Carnivora	Felidae	Wild	NT	1	(25)
148	*Papio ursinus*	Primates	Cercopithecidae	Wild	LC	NA	(18)
149	*Paracynictis selousi*	Carnivora	Herpestidae	Wild	LC	NA	(18)
150	*Phyllostomus hastatus*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
151	*Pipistrellus hesperus*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
152	*Pipistrellus kuhlii*	Chiroptera	Vespertilionidae	Wild	LC	NA	(18)
153	*Pipistrellus subflavus*	Chiroptera	Vespertilionidae	Wild	LC	1	(21)
154	*Plecotus auritus*	Chiroptera	Vespertilionidae	Wild	LC	NA	(18)
155	*Pongo pygmaeus*	Primates	Hominidae	Wild	EN	NA	(18)
156	*Procavia capensis*	Hyracoidea	Procaviidae	Wild	LC	NA	(18)
157	*Procyon lotor*	Carnivora	Procyonidae	Wild	LC	1	(13)
158	*Proteles cristata*	Carnivora	Hyaenidae	Wild	LC	1	(25)
159	*Pseudalopex vetulus*	Carnivora	Canidae	Wild	LC	1	(13)
160	*Pteronotus davyi*	Chiroptera	Mormoopidae	Wild	LC	1	(13)
161	*Pteronotus parnellii*	Chiroptera	Mormoopidae	Wild	LC	0	(22)
162	*Pteropus poliocephalus*	Chiroptera	Pteropodidae	Wild	VU	1	(13)
163	*Rangifer tarandus*	Cetartiodactyla	Cervidae	Wild	LC	1	(13)
164	*Rhinolophus ferrumequinum*	Chiroptera	Rhinolophidae	Wild	LC	0	(13)
165	*Rhinolophus pusillus*	Chiroptera	Rhinolophidae	Wild	LC	0	(13)

Table II (cont.)

	Reported host species	Order	Family	Wild or domestic status	IUCN Red List status	Detection method*	Reporting source
166	*Rousettus leschenaultii*	Chiroptera	Pteropodidae	Wild	LC	0	(13)
167	*Saimiri sciureus*	Primates	Cebidae	Wild	LC	NA	(18)
168	*Sciurus carolinensis*	Rodentia	Sciuridae	Wild	LC	0	(13)
169	*Sciurus niger*	Rodentia	Sciuridae	Wild	LC	0	(13)
170	*Spermophilus tridecemlineatus*	Rodentia	Sciuridae	Wild	LC	0	(13)
171	*Spermophilus undulatus*	Rodentia	Sciuridae	Wild	LC	1	(13)
172	*Spermophilus variegatus*	Rodentia	Sciuridae	Wild	LC	0	(13)
173	*Sturnira lilium*	Chiroptera	Phyllostomidae	Wild	LC	0	(13)
174	*Suncus murinus*	Eulipotyphla	Soricidae	Wild	LC	NA	(18)
175	*Suricata suricatta*	Carnivora	Herpestidae	Wild	LC	1	(23)
176	*Sus scrofa*	Cetartiodactyla	Suidae	Domestic	LC	1	(18)
177	*Tadarida brasiliensis*	Chiroptera	Molossidae	Wild	LC	1	(21)
178	*Tamias striatus*	Rodentia	Sciuridae	Wild	LC	0	(13)
179	*Taurotragus oryx*	Cetartiodactyla	Bovidae	Wild	NE	NA	(18)
180	*Tragelaphus strepsiceros*	Cetartiodactyla	Bovidae	Wild	LC	1	(13)
181	*Urocyon cinereoargenteus*	Carnivora	Canidae	Wild	LC	0	(13)
182	*Uroderma bilobatum*	Chiroptera	Phyllostomidae	Wild	LC	1	(13)
183	*Vespertilio murinus*	Chiroptera	Vespertilionidae	Wild	LC	1	(13)
184	*Vulpes chama*	Carnivora	Canidae	Wild	LC	NA	(18)
185	*Vulpes corsac*	Carnivora	Canidae	Wild	LC	1	(13)
186	*Vulpes lagopus*	Carnivora	Canidae	Wild	LC	NA	(18)
187	*Vulpes velox*	Carnivora	Canidae	Wild	LC	0	(13)
188	*Vulpes vulpes*	Carnivora	Canidae	Wild	LC	1	(13)
189	*Vulpes zerda*	Carnivora	Canidae	Wild	LC	NA	(18)
190	*Xerus inauris*	Rodentia	Sciuridae	Wild	LC	NA	(18)

*Detection method:
0: Only serology reported
1: Polymerase chain reaction or viral isolation reported
NA: detection method not reported/confirmed

DD: Data deficient
EN: Endangered
IUCN: International Union for Conservation of Nature
LC: Least concern

NE: Not evaluated
NT: Near threatened
VU: Vulnerable

Table III

Conservation status of mammalian host species in which infection with rabies virus was reported, as classified in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species

IUCN Red List Status	No. of infected species reported
Endangered (EN)	7
Vulnerable (VU)	5
Near threatened (NT)	4
Least concern (LC)	156
Data deficient (DD)	6
Not evaluated (NE)	12

IUCN: International Union for Conservation of Nature

The social and feeding behaviours of the African wild dog promote opportunities for rapid RABV spread, leading to the loss of entire packs in East Africa (39, 40). Consistent with the Allee effect, since their overall population size is already limited, high-density packs may have a minimum threshold below which the risk of extinction increases (41).

In Ethiopia, the Bale Mountain population of the Ethiopian wolf, which constitutes the majority of the estimated fewer than 500 individuals left of the species worldwide, suffered a population decline of ~60% in the early 1990s, from an RABV outbreak (38). Domestic dogs are considered to be the source of RABV in these outbreaks (38, 42). Although the Ethiopian wolf population has subsequently rebounded, signs of recovery after the 1990/1991 outbreak were not evident for four or more years, with full recovery taking approximately a decade (43). The habitat of this endangered species is already highly fragmented and confined to an ecosystem of limited geographical range, presenting parallel pressures and potentially affecting population density trends that may enhance the Ethiopian wolf's vulnerability to rabies (44).

Rabies virus has been documented in other carnivore species with an elevated extinction risk, many of which have experienced population declines as a result of persecution due to perceived threats to livestock; habitat destruction; and/or subsequent increased interaction with domestic species. Early records report rabies epidemics in dholes (*Cuon alpinus*) that led to human fatalities (40, 45), suggesting a strong potential for both inter- and intra-species transmission. Occasional rabies cases have been reported in wild African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*A. jubatus*) (18, 20, 46, 47, 48). Predation on or conflict with domestic dogs has been proposed as a source of infection in some of these cases (49). There are limited reports of rabies in the black-footed cat (*Felis nigripes*), striped hyena (*Hyaena hyaena*) and maned wolf (*Chrysocyon brachyurus*) (18, 23, 26). African mongoose RABV variants have been identified in at least one black-footed cat, indicating the possible relevance of sylvatic reservoirs and natural food sources for RABV infection of this species (23). The ecology of RABV in the striped hyena warrants investigation, as a preference for areas inhabited by humans and a tendency to kill dogs (50) are two factors that may increase the risk of RABV transmission from domestic dogs to striped hyena, and from striped hyena to humans. The authors found one report of RABV in maned wolves, detected via serology, indicating the possibility of non-fatal infection in individuals (26). However, the overall impact of RABV infection on populations of maned wolves is not well clarified.

Non-carnivore species of conservation concern have also been affected by RABV from domestic dog reservoirs. RABV has been reported sporadically in Asian elephants (*Elephas maximus*) (18, 51, 52, 53). The majority of such reports implicate rabid domestic dogs as the source of infection, particularly in areas where there is an absence of locally circulating sylvatic strains (29). The potential for intra-species transmission of RABV within Asian elephant populations is not known; the authors could find no reports of this in the literature. However, cases of RABV and repeat encounters with infected dogs have the potential to reduce the already shrinking numbers of this endangered species, which have been in decline as a consequence of poaching and human–animal conflict, as well as habitat fragmentation and loss (54, 55).

There are very few reports in the literature of rabies in primates of elevated IUCN conservation status. The authors found reports of infection only in the Lars gibbon (*Hylobates lar*) and orangutan (*Pongo pygmaeus*) (18). The information available on rabies in other non-human primate species comes from species that are geographically and ecologically different (e.g. marmosets in Brazil [*Callithrix jacchus*]), which have unique circulating variants (56).

Rabies virus circulates differently within bat populations as compared to within terrestrial mammals. While the direct impact of RABV on bat population declines is not clear, several vulnerable or endangered bat species have been reported as testing RABV-positive in select cases. These species include the greater long-nosed bat (*Leptonycteris nivalis*), the southern long-nosed bat (*Leptonycteris curasoae*), the grey bat (*Myotis grisescens*) and the grey-headed flying fox (*Pteropus poliocephalus*) (21, 22, 27). While it should be noted that the report of the grey-headed flying fox is probably due to cross-reactivity with lyssaviruses, populations of all these species are decreasing, due to habitat disturbance or destruction and reduced food availability (20, 22, 27, 57, 58, 59).

Establishment of rabies virus in novel hosts

Rabies virus in domestic dogs poses an ongoing threat to animal health through the establishment of an RABV reservoir in a novel host species. For example, the emergence of RABV in the crab-eating fox (*Cerdoyon thous*) has been phylogenetically linked to RABV of domestic dog origin and spillover infection of foxes in the early 1900s (60). Similarly, 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 (61, 62).

Human activities can affect wild animal populations in ways that may encourage the establishment of sylvatic reservoirs in new environments. For example, populations of the Indian mongoose (*Herpestes auropunctatus*), introduced into the Caribbean in the mid-19th century for pest control, now maintain RABV independently on several islands and are one of the primary RABV reservoirs in the region. The RABV strains recorded in Cuba and Puerto Rico share their lineage with that of a dog-derived RABV, but differ genetically from strains found in mongoose species elsewhere in the world, suggesting that their strain originated from domestic dogs (63, 64). Similarly, the raccoon dog (*Nyctereutes procyonoides*), introduced into western Russia for fur farming (65), now serves as one of the leading wild animal RABV reservoirs in some countries, including Poland and Finland (65, 66).

In Latin America, deforestation for agriculture and intensified cattle farming have led to increases in vampire bat (*Desmodus rotundus*) populations. Vampire bats have become the major sylvatic RABV reservoir in this region, with cattle as their preferred food source (67, 68).

As demonstrated by analyses of the geographical and inter-species spread of RABV, monitoring virus phylogeny provides valuable information with which to identify the source of virus strains and the selection pressures leading to host shifts, to help to refine prediction, prevention and control strategies (11, 69). This information is not always reported with surveillance testing or in the literature. A better understanding of the particular strain of RABV concerned, through genetic analysis or antigenic typing, can help to elucidate virus strain ecology.

Control measures

Efforts to reduce the threat of rabies to wildlife must be targeted to address endemic sylvatic cycles of infection and domestic dog strains. Uncertainty around RABV strain ecology presents challenges when trying to determine appropriate management approaches (70); this may be especially pertinent to wild animals with complex ecologies. As a result, inappropriate control measures, such as reducing wildlife populations through shooting incentives or fumigation, may be taken (71). In Latin America, the control of vampire bat populations has included culling bats using an anticoagulant paste, which is then dispersed to the colony through mutual grooming (72, 73). These bat-culling activities may be ineffective or counterproductive in decreasing the prevalence of rabies among these populations (74, 75).

In addition, two other vampire bat species (*Diaemus youngi* and *Diphylla ecaudata*), which are not known to feed on mammals and are thus not implicated in RABV transmission, may also fall victim to culling efforts (76). Culling has also been shown to be ineffective in controlling canine and fox rabies (77, 78), as well as more broadly in efforts to control other infectious diseases (79, 80).

Vaccination campaigns in wildlife can be laborious and logistically challenging (81, 82). Some campaigns target extensive numbers of individuals relative to the numbers of reported cases. For example, one intervention involved ring vaccination targeted at nearly 140,000 animals for 22 reported cases of rabies in red foxes (*Vulpes vulpes*) in 2013 (18).

These campaigns can also be expensive. An oral rabies vaccination (ORV) campaign conducted in wild animals in North America, between 1999 and 2009, was estimated to have cost at least $130 million (combined Canadian and United States dollars), and the cost of Europe's ORV campaign targeting red foxes was estimated at nearly €400 million, for programmes in 22 European countries, initiated between 1978 and 2009 (61, 82). However, in some cases, wildlife vaccination was shown to be a cost-effective prevention and control strategy (83), and has contributed to significant savings, when animal vaccination costs are compared to the costs of human post-exposure prophylaxis (PEP) treatment (84).

The elimination of terrestrial RABV is the current target of efforts in Central Europe and parts of the Americas, with a shared global vision of eliminating canine rabies by 2030 (85). Historically, in Europe, administering ORV has been effective in controlling rabies in foxes after control has been achieved in domestic animals. Although rabies in domestic and wild animals still persists in some Eastern European countries (61, 85), most European countries are now rabies free, due to its control in domestic animals through dog vaccination and ORV campaigns to eliminate the virus in red foxes. Marked progress occurred on the continent once vaccination was scaled up geographically and included connected areas (86, 87). Lithuania and Latvia recently eradicated terrestrial RABV in wildlife and domestic animal rabies with these strategies (88).

In the United States of America (USA), now that domestic animal rabies has been effectively controlled, 92% of reported rabies cases occur in wild animals (89), with raccoons (*Procyon lotor*), foxes, coyotes (*Canis latrans*), and skunks (*Mephitis mephitis*) serving as the primary terrestrial reservoirs. Current control efforts in wild animals involve the annual delivery of vaccine-laden baits to terrestrial wild animals, paired with nationwide testing and reporting (30). However, bats represent the main source of transmission to humans in the USA, suggesting that a substantial proportion of wild animal infections may be missed in routine wildlife surveillance and reporting (90). Bats also remain a challenging taxon for the application of control measures (91).

Large-scale dog vaccination and dog population control can be successful measures in rabies elimination programmes and can reduce the spread of domestic canine RABV to wild animals (92). Dog vaccination and population control serve to eliminate rabies within the primary RABV reservoir, reducing the likelihood of exposure of other species. Where they have been applied consistently, mass vaccination campaigns have been the single most cost-effective intervention in controlling canine rabies (42), and their benefits are extended to wildlife affected by dog-strain rabies (92). The elimination of dog-mediated rabies is a target of the OIE, the World Health Organization (WHO) and FAO (93).

However, this method has not achieved RABV control in parts of Africa and Asia, due – at least in part – to a lack of awareness, misperceptions of its epidemiological feasibility, and constraints on operational planning, implementation and resources (94). In areas where mass dog vaccination has brought about the near-elimination of canine RABV, attention can then be turned towards the role of wild animals as reservoirs of RABV, to determine if control or risk mitigation strategies in wildlife are feasible or warranted.

Conclusions

Rabies, and infectious diseases in general, may be an added pressure on animal populations already endangered by other drivers of biodiversity loss, potentially accelerating population declines towards extinction (1). Ecological changes often result in altered pathogen transmission dynamics; for example, the introduction of domestic dogs may carry rabies into new territories or modify host feeding preferences, resulting in interspecies transmission. Wild animals living at habitat borders may be most directly susceptible, due to their proximity to domestic canids. Spillover from dogs to wild animals at the edges of protected and forested areas has been seen with canine distemper virus and linked to a major population decline of Serengeti lions (*Panthera leo*) in Kenya. Spillover is also apparent with canine parvovirus detected in wildlife, including fox, opossum and raccoon species, in the Argentinian Chaco (95, 96, 97).

Efforts to control rabies in wild animals may be of limited short-term use if a continuing source of RABV introduction from domestic dogs is not also addressed. Controlling RABV in domestic dogs, through mass vaccination, dog population control, education in dog-bite prevention and treatment, and the appropriate use of human PEP, is known to be effective in preventing 99% of human cases and eliminating the most common source of disease introduction to wild animals (98). Thus, controlling RABV in domestic dogs should be a priority for rabies control and prevention in human and wildlife populations.

Where RABV strains are maintained independently in wildlife populations, dog vaccination may still be important for preventing the potential introduction of RABV from other reservoirs (64). A step-by-step approach to rabies control, beginning with consistent canine rabies control and followed by a determination of needs and feasibility for wildlife rabies control, must consider local ecological dynamics and target ecologically appropriate species (94, 99, 100).

Correct identification of RABV strains through consistent typing can also support efforts to bolster knowledge on rabies transmissibility, ecological links, pathogenicity and control, thus providing a basis for enhanced collaboration among the human, domestic animal and wild animal health communities. Mathematical models of RABV transmission that incorporate wild animal data to investigate intra- and interspecies transmission dynamics and the cost-effectiveness of management approaches may also provide a greater understanding of RABV strain dynamics and afford opportunities for conservation management. Similarly, ongoing monitoring and surveillance of wildlife for pathogens, including RABV, are crucial to enable early detection, identify where disease introductions may be occurring, and to promote effective management strategies (81).

The elimination of canine rabies remains a priority for the Tripartite (OIE, FAO and WHO), using the 'One Health' approach, which involves multidisciplinary collaboration between the human health and animal health sectors, among others. The elimination of canine rabies will improve both public and veterinary health, as well as benefit biodiversity.

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La rage en tant que menace pour la faune sauvage

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Résumé

L'impact des maladies infectieuses peut constituer une menace croissante pour la survie d'espèces animales sauvages dès lors que leurs populations sont entraînées dans la « spirale de l'extinction ». Ce risque se pose plus particulièrement lorsqu'il s'agit d'agents pathogènes qui se propagent rapidement et induisent un taux de mortalité élevé. Le virus de la rage affecte un grand nombre d'espèces de mammifères et se transmet facilement par contact avec de la salive infectée ; l'infection virale entraîne la mort en l'absence d'une vaccination préalable ou, chez l'être humain, d'une prophylaxie post-exposition administrée rapidement. Les auteurs ont procédé à un examen exhaustif de la littérature afin d'inventorier les espèces de mammifères sauvages chez qui l'infection rabique a été rapportée. Des cas ont été notifiés chez 190 espèces de mammifères, dont 16 présentant un risque élevé d'extinction et deux directement menacées d'extinction en raison de la rage : le loup d'Abyssinie *(Canis simensis)* et le lycaon *(Lycaon pictus)*. Les auteurs apportent des précisions sur un nombre choisi d'espèces vulnérables ou en danger dont le déclin des populations est en partie imputé à la rage. En outre, ils soulignent l'importance de la transmission du virus de la rage des chiens domestiques aux animaux sauvages et décrivent les nombreuses difficultés liées à la vaccination de la faune sauvage. Ces éléments établis, ils présentent quelques solutions envisageables pour réduire le fardeau de la rage dans la faune sauvage. Une fois le virus de la rage contrôlé de manière pérenne chez le chien domestique il sera possible de lutter plus efficacement contre les autres menaces que la rage fait peser sur la conservation de la faune.

Mots-clés

Biodiversité – Chien domestique – Conservation – Extinction – Faune sauvage – Rage – Une seule santé – Vaccination.

■

La rabia, una amenaza para la fauna silvestre

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Resumen

Una enfermedad infecciosa puede tener efectos cada vez más dañinos en la supervivencia de una especie a medida que una población silvestre se va aproximando a un «vórtice de extinción». Este riesgo tiene especial importancia en el caso de patógenos que se propagan con rapidez y causan elevadas tasas de mortalidad. La rabia, enfermedad provocada por un virus que infecta a muchas especies de mamíferos y puede transmitirse eficazmente a través de saliva infectada, resulta letal en ausencia de vacunación previa o de rápidas medidas de profilaxis tras la exposición (en el ser humano). Los autores realizaron un amplio estudio bibliográfico para determinar todas aquellas especies de mamíferos silvestres en que se hubiera descrito una infección por el virus de la rabia. Encontraron infecciones descritas en 190 especies de mamíferos, de las que 16 presentan un elevado riesgo de extinción y dos cuya conservación se ve directamente amenazada por la rabia: el lobo etíope *(Canis simensis)* y el licaón, o perro salvaje africano *(Lycaon pictus)*. Los autores exponen una serie de ejemplos en los que la rabia ha contribuido al declive demográfico de una especie cuya pervivencia está en mayor o menor peligro. Los autores señalan además la importancia que reviste la transmisión del virus de la rabia de los perros domésticos a la fauna silvestre y los numerosos problemas que presenta la vacunación de los animales silvestres. Teniendo presente esta dificultad, exponen posibles soluciones para reducir la carga de rabia en la fauna silvestre. Una vez se logre estabilizar el control del virus rábico en el perro doméstico, será posible combatir más eficazmente la amenaza que representa para la conservación de las especies silvestres.

Palabras clave

Biodiversidad – Conservación – Extinción – Fauna silvestre – Perro doméstico – Rabia – Una sola salud – Vacunación.

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