

RABIES AMONG INFREQUENTLY REPORTED MAMMALIAN CARNIVORES IN THE UNITED STATES, 1960–2000

Authors: Krebs, John W., Williams, Sarah M., Smith, Jean S.,

Rupprecht, Charles E., and Childs, James E.

Source: Journal of Wildlife Diseases, 39(2): 253-261

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-39.2.253

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

RABIES AMONG INFREQUENTLY REPORTED MAMMALIAN CARNIVORES IN THE UNITED STATES, 1960–2000

John W. Krebs,^{1,2} Sarah M. Williams,¹ Jean S. Smith,¹ Charles E. Rupprecht,¹ and James E. Childs¹

¹ Division of Viral and Rickettsial Diseases, Centers for Disease Control and Prevention, Public Health Service, US Department of Health and Human Services, 1600 Clifton Road MS/G13, Atlanta, Georgia 30333, USA

² Corresponding author (email: jok2@cdc.gov)

ABSTRACT: Most cases of rabies reported annually in the United States occur among three groups of carnivores—raccoons (*Procyon lotor*), skunks (*Mephitis, Spilogale*, and *Putorius*), foxes (*Vulpes, Urocyon*, and *Alopex*)—and among bats (numerous species). However, between 1960 and 2000, a total of 2,851 cases of rabies in 17 other carnivore taxa were reported to the Centers for Disease Control and Prevention, Atlanta, Georgia (USA), from 49 states, the District of Columbia, and Puerto Rico. Three species of these other carnivores (mongooses [*Herpestes javanicus*], coyotes [*Canis latrans*], and bobcats [*Lynx rufus*]) accounted for 92% (2,624/2,851) of the cases reported among other canivorous mammals (OCMs). Most OCMs demonstrated temporal or spatial variation in numbers of reported cases. Tests of specimens from OCMs infected in the United States identified variants of the rabies virus that corresponded with variants associated with the major terrestrial reservoirs within their respective regions of origin. Variants of the rabies virus in samples from mongooses in Puerto Rico could not be distinguished from those in samples from dogs in Puerto Rico by virus typing methods.

Key words: Carnivora, Canis latrans, coyote, Herpestes auropunctatus, Herpestes javanicus, infrequent reports, mongoose, rabies, rabies distribution, rabies surveillance.

INTRODUCTION

Certain groups of terrestrial carnivores indigenous to the United States are known to function as reservoirs for rabies virus and serve as maintenance hosts for specific virus variants that can be distinguished by their antigenic and genetic characteristics (Smith et al., 1995). The major hosts include raccoons (Procyon lotor), skunks (genera Mephitis, Spilogale, and Putorius), and foxes (genera Vulpes, Urocyon, and Alopex) (Krebs et al., 2000, 2001). Additional and extensive reservoirs for rabies virus exist among the numerous species of insectivorous bats which maintain a diverse pool of rabies virus variants that circulate independently of those associated with terrestrial carnivores (Baer and Smith, 1991). Rabies reported among raccoons, skunks, foxes, and bats accounted for 91% of all cases of rabies during 2000; domestic species (including dogs) contributed less than 7% to the total. Thirteen other species of wildlife made up the remaining 2% of nationally reported rabies

In any given geographic region of the

United States where rabies is enzootic, most cases of rabies are caused by the rabies virus variant associated with the primary terrestrial carnivore host in that region (McQuiston et al., 2001). As of 2002, nine variants of rabies virus identifiable by antigenic or genetic typing methods are know to circulate among terrestrial carnivores in the United States and Puerto Rico (Smith, 1989, 1995). Three variants are associated with skunks, three with foxes, and one with raccoons. Two other carnivores are important in maintaining distinct rabies virus variants that currently circulate in restricted regions of the United States: coyotes (Canis latrans) in southern Texas (Rohde et al., 1997) and mongooses (Herpestes javanicus [auropunctatus]) on Puerto Rico (Krebs et al., 2001).

Although reports of rabies among carnivores other than the primary reservoir host species are rare, other carnivorous mammals (OCMs) can be a source of rabies exposure to humans and domestic animals. Annual national surveillance reports of rabies list most of these other wildlife species without attempting to summarize

any long-term trends in numbers or geographic occurrence. In this report, we review rabies surveillance data for the period between 1960 and 2000 for OCMs that were less frequently reported rabid in the United States than are raccoons, skunks, and foxes. In some instances (e.g., coyotes and mongooses), these carnivores are of regional importance and serve as primary host species in virus maintenance, while for other species reports of rabies are rare and reflect spillover infections.

MATERIALS AND METHODS

Between January 1960 and December 2000, state and territorial health departments reported confirmed cases of rabies to the Centers for Disease Control and Prevention (CDC) on a monthly basis. Data on animal rabies compiled at CDC dates to 1960, although details on the reporting of cases to the county level are complete only back to 1990 for most species. The diagnosis of rabies was made at state laboratories or at CDC, usually by direct fluorescent antibody testing. In some instances, mouse inoculation with brain tissue from the suspected animal or reverse transcription-polymerase chain reaction (RT-PCR) assays of tissues or fluids were used to detect virus or viral RNA. Characterizations of the rabies virus variants associated with cases were performed using antigenic typing with monoclonal antibodies or RT-PCR, followed by genetic sequencing.

Reported cases of rabies in OCMs from 1960 through 2000 were examined for temporal and spatial patterns. Identification of OCMs was made to the level of species when possible, although bears were recorded only to genus Ursus and weasels were recorded only to genus Mustela. Data were grouped by decade (1960-1969, 1970-1979, 1980-1989) with the exception of the last interval (1990-2000), which was 11 yr in duration. Data were also grouped by surveillance region to look for geographic clustering. Regions were defined as the standard surveillance groups used by CDC: New England (Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, Vermont), mid-Atlantic (New Jersey, New York, Pennsylvania), North Central (Iowa, Illinois, Indiana, Kansas, Michigan, Minnesota, Missouri, North Dakota, Nebraska, Ohio, South Dakota, Wisconsin), South Atlantic (Washington D.C., Delaware, Florida, Georgia, Maryland, North Carolina, South Carolina, Virginia, West Virginia), South Central (Alabama, Arkansas, Kentucky, Louisiana, Mississippi, Oklahoma, Tennessee, Texas),

Mountain (Arizona, Colorado, Montana, New Mexico, Nevada, Utah, Wyoming), Pacific (Alaska, California, Hawaii, Oregon, Washington), and Territories (Guam, Puerto Rico, Virgin Islands, American Samoa).

RESULTS

A total of 2,851 cases of rabies among OCMs of at least 17 different species were reported from 1960 through 2000 (Table 1). This total represented 1.3% of the 216,212 cases of animal rabies reported to CDC during this same interval and 1.5% of the 185,014 wildlife cases. Three species accounted for 92% of the total reported rabies cases among OCMs. Mongooses contributed almost 53% of the total, followed by coyotes (22%) and bobcats (Lynx rufus; 17%). Four other species contributed >1% to the total number of rabies cases among OCMs: otters (Lontra canadensis; n=45 cases), badgers (Taxidea taxus; n=40 cases), wolves (Canis lupus; n=31 cases), and ringtails (Bassariscus astutus; n=29 cases). The remaining 10 species or groups of OCMs collectively accounted for <3% of the total OCM rabies

Overall, the number of reported rabies cases among OCMs increased gradually during the first three decades of study, from 1960 to 1989 (average for the 30-yr interval = 53.5 OCM rabies cases per year), before doubling between 1990 and 2000 (average for the 11-yr interval = 113.4 OCM rabies cases per year). This marked increase was driven by a well-defined epizootic of rabies among coyotes occurring in southern Texas during the early 1990s (Fig. 1) and a nearly fivefold increase in the numbers of rabid bobcats (n=240) over the number reported from the previous decade, 1980–1989 (n=51)(Table 1).

Reports of rabies among several different species of OCMs have increased since 1960. The numbers of mongooses reported rabid increased over 300% from 1960 to 1989 (n=161 for the 1960s, 360 for the 1970s, and 493 for the 1980s) before leveling-off during the 1990s (n=493). Re-

Species or genus	1960–1969	1970–1979	1980–1989	1990-2000	Total
Mongoose Herpestes javanicus	161	360	493	493	1,507
Coyote Canis latrans	81	76	45	427	629
Bobcat Lynx rufus	140	57	51	240	488
Otter Lontra canadensis	1	3	5	36	45
Badger Taxidea taxus	13	5	15	7	40
Wolf Canis lupus	9	5	11	6	31
Ringtail Bassariscus astutus	9	8	4	8	29
Domestic ferret Mustela putorius	0	1	11	11	23
Coati Nasua narica	5	5	2	0	12
Mink Mustela vison	4	4	0	3	11
Weasel Mustela spp.	2	5	3	1	11
Fisher Martes pennanti	1	1	0	6	8
Wolf-dog hybrid Canis lupus ×					
C. lupus familiaris	0	0	0	5	5
Puma Puma concolor	1	1	1	1	4
Bear <i>Ursus</i> spp.	0	1	0	3	4
Lesser panda Ailurus fulgens	0	0	3	0	3
Ocelot <i>Leopardus pardalis</i>	1	0	0	0	1
Total	428	532	644	1,247	2,851

TABLE 1. Cases of rabies among selected carnivores reported from the United States and territories, 1960–2000, ranked by contribution to the total.

ports of rabies among otters and domestic ferrets (*Mustela putorius*) have increased from historical lows in recent decades. However, the overall number reported for these two species has averaged <2 per year over the entire study interval (Table 1). Rabies among wolf-dog hybrids was reported for the first time during the 1990s (Table 1).

Regional distribution of OCM rabies cases varied and in most instances was interpretable based on the known geograph-

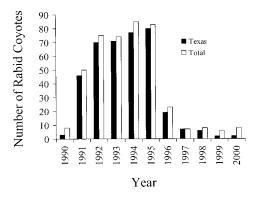


FIGURE 1. Annually reported cases of rabies in coyotes for Texas and the remainder of the United States, 1990–2000.

ic range of the species (Table 2). For example, all reports of rabid mongooses originated from Puerto Rico, although reporting varied from different locations on the island. Between 1990 and 2000, townships in the eastern end of the island reported most of the cases of mongoose rabies (Fig. 2). Other reports of rabies among OCMs that were restricted regionally included those for badgers, wolves, ringtails, and coatis (*Nasua narica*) (Table 2).

In contrast, some OCMs have extensive range distributions and rabies was reported among these animals throughout their range. The South Central Region accounted for 71.4% of the rabid coyotes reported since 1960 (Fig. 3a); however, this species was found rabid in every region of the continental United States. Similarly, although most rabid bobcats (44.9%) were reported from the South Atlantic and South Central regions (22.4%), cases of rabies in this species occurred in every region of the continental US (Fig. 3b). Most cases (73.3%) of rabies among otters were reported from the South Atlantic Region (Table 2), but they occur throughout much of the conti-

	•								
Species or genus	NEngla	Mid- Atl ^a	NCnta	SAtla	SCnt ^a	Mtna	Pefa	Ttry ^a	Total
Mongoose Herpestes javanicus	0	0	0	0	0	0	0	1,507	1,507
Coyote Canis latrans	12	16	47	7	449	67	31	0	629
Bobcat Lynx rufus	5	10	6	219	141	64	43	0	488
Otter Lontra canadensis	2	5	0	33	0	0	5	0	45
Badger Taxidea taxus	0	0	30	0	1	4	5	0	40
Wolf Canis lupus	0	0	5	0	5	0	21	0	31
Ringtail Bassariscus astutus	0	0	0	0	23	5	1	0	29
Domestic ferret Mustela putorius	1	4	6	10	1	0	1	0	23
Coati Nasua narica	0	0	0	1	1	10	0	0	12
Mink Mustela vison	0	0	6	3	2	0	0	0	11
Weasel Mustela spp.	1	0	3	1	5	1	0	0	11
Fisher Martes pennanti	6	2	0	0	0	0	0	0	8
Wolf-dog hybrid Canis lupus ×									
C. lupus familiaris	0	0	0	0	1	0	4	0	5
Puma Puma concolor	0	0	0	1	0	2	1	0	4
Bear Ursus spp.	0	2	0	0	0	2	0	0	4
Lesser panda Ailurus fulgens	0	0	0	3	0	0	0	0	3
Ocelot Leopardus pardalis	0	0	0	0	0	0	1	0	1
Total	27	39	103	278	629	155	113	1,507	2,851

TABLE 2. Cases of rabies among selected carnivores reported from different regions of the United States and territories, 1960–2000, ranked by contribution to the total.

nental United States. Six of the seven regions within the continental United States reported at least one case of rabies among domestic ferrets, although 10 of the 23 cases originated from the South Atlantic Region (Table 2). Four of the five cases of rabies in wolf-dog hybrids were from the Pacific Region.

Virus typing was conducted on 66 samples collected between 1985 and 1998 (Table 3). Each of the major US geographic regions were represented among the samples, which were taken from 11 species of

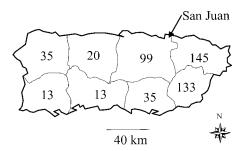


FIGURE 2. Reported cases of rabies in mongooses in Puerto Rico, by township, 1960–2000.

OCMs originating from 18 states, the District of Columbia (D.C.), and Puerto Rico. All nine of the virus variants associated with terrestrial animal reservoirs for rabies in the US were identified among the 66 samples within this time interval, including arctic fox, raccoon (Mid-Atlantic and Southeast United States), south central (SC) skunk, north central (NC) skunk, Arizona (AZ) fox, California (CA) skunk, Texas (TX) fox, Mexico (MX) dog, and Puerto Rico (PR) mongoose/dog. Two samples from ringtails submitted for rabies testing in Nevada and New Mexico contained variants associated with bats (Pipistrellus hesperus and Tadarida brasiliensis, respectively).

DISCUSSION

Although the OCMs reviewed in this report contributed less than 2% to the burden of wildlife rabies reported in the United States between 1960 and 2000, these species can be a source of human and domestic animal exposure to rabies virus. Ra-

a NEngl=New England; MidAtl=MidAtlantic; NCnt=North Central; SAtl=South Atlantic; SCnt=South Central; Mtn=Mountain; Pcf=Pacific; Ttry=Territories. See text for states in each region.

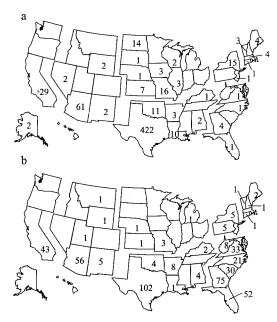


FIGURE 3. Reported cases of rabies in coyotes (a) and bobcats (b), by surveillance region, United States, 1960–2000.

bies among terrestrial mammals other than raccoons, skunks, and foxes represents the dominant threat in certain locations, and disease occurs with sufficient magnitude as to warrant a public health intervention.

For example, the epizootic of coyote rabies in southern Texas (Fig. 1) involved a variant of rabies virus that had been circulating among domestic dogs along the Mexico-United States border at least since the 1970s (Clark et al., 1994; Smith et al., 1995; Rohde et al., 1997). Two human deaths in Texas, in 1991 and 1994, were attributed to this rabies virus variant (Noah et al., 1998). Once this virus variant became established within the coyote population, it rapidly emerged in several adjacent counties (Clark et al., 1994), raising local and national concerns over the potential for epizootic spread. Coyotes can be found throughout the US in all habitats (Moore and Parker, 1992), and the potential for a spreading epizootic of coyote rabies, involving a variant of the virus well adapted to circulation in domestic dogs, to affect large regions of Texas and other areas in the US was regarded as a clear pub-

lic health threat. In an attempt to halt the further spread of this variant of the rabies virus, a program was initiated to vaccinate coyotes in south Texas by using an oral rabies virus vaccine (ORV) distributed in edible baits (Farry et al., 1998; Fearneyhough et al., 1998). As of 2000, the distribution of ORV had been credited with reducing the numbers of rabid coyotes in south Texas and halting the further spread of rabies associated with this species (Farry et al., 1998). Similarly, development of suitable baits and ORV delivery strategies for vaccinating mongooses on islands in the Caribbean are under way (Linhart et al., 1993; Creekmore et al., 1994).

Cases of rabies among bobcats were reported during all periods and from all regions. However, temporally, the majority were reported during the 1960s and the 1990s, and regionally >85% were reported from southern states. Variants of the rabies virus identified in bobcats from the South Atlantic states were uniformly the raccoon rabies virus strain, while variants from bobcats in Arizona and Texas were predominantly respective regional fox variants (one was SC skunk). Unproven hypotheses regarding causes for the predominance of infection of bobcats with fox variants range from the possibility of greater numbers of encounters as a result of mutual climbing skills of the species involved to the possibility that foxes may fall among those species preyed upon by bobcats. Absence of information about rabies virus variants that infected foxes during the 1960s does not allow confirmation of the possibility that the greater numbers of rabid bobcats reported during that period were the result of the more expansive epizootic of rabies among foxes. Resurgence of reported cases of rabies among bobcats during the 1990s to the present is primarily caused by spillover of rabies as a result of epizootics among raccoons in the southeastern states.

Rabies among some OCMs has been regarded more as a threat to the survival of a rare or endangered species (MacDonald, 1993), or a potential problem affecting the

TABLE 3. Rabies virus variants typed from carnivore samples in different regions of the United States and territories. Almost all the virus variants were those circulating among the predominant terrestrial wildlife reservoirs with the exception of two ringtails.

Region ^a	States	Species tested (n)	Rabies virus variant (terrestrial) ^b	Rabies virus variant (bat)	
NEngl	NY (1)	coyote (1)	arctic fox (1)		
	CT (1)	ferret (1)	raccoon (1)		
	NH (1)	fisher (1)	raccoon (1)		
MidAtl	NJ (2)	ferret (2)	raccoon (2)		
NCnt	IA (1)	ferret (1)	NC skunk (1)		
SAtl	GA (3), FL (1), VA (1), WV (1)	bobcat (6)	raccoon (6)		
	FL (1)	coyote (1)	raccoon (1)		
	VA (1), DC (1), FL (1)	ferret (3)	raccoon (3)		
	VA (1)	mink (1)	raccoon (1)		
	FL (1)	puma (1)	raccoon (1)		
	DE (1), GA (1)	otter (2)	raccoon (2)		
	DC (3)	panda (3)	raccoon (3)		
SCnt	TX (5)	bobeat (5)	TX fox or MX dog (4) ^c		
			SC skunk (1)		
	AL (1)	coyote (1)	raccoon (1)		
	AR (1)	coyote (1)	SC skunk		
	TX (18)	coyote (18)	TX fox or MX dog (18) ^c		
	AR (1)	ferret (1)	SC skunk		
Mtn	AZ(4)	bobcat (4)	AZ fox (4)		
	AZ(3)	coyote (3)	AZ fox (3)		
	NV (1), NM (1)	ringtail (2)		bat PH (1) ^d bat TB (1) ^d	
Pef	CA (3)	wolf-dog hybrid (3)	CA skunk (3)	Dat 1B (1)	
	CA (1)	covote (1)	MX dog (1)		
	CA (1)	ferret (1)	CA skunk (1)		
	CA (1)	puma (1)	CA skunk (1)		
Ttry	PR (2)	mongoose (2)	PR mongoose/dog (2)		

^a NEngl=New England; MidAtl=MidAtlantic; NCnt=North Central; SAtl=South Atlantic; SCnt=South Central; Mtn=Mountain; Pcf=Pacific; Ttry=Territories. See text for states in each region.

sustainable harvest of furbearer species (Clark and Fritzell, 1992), than as a public health issue (Kimber et al., 2000). An epizootic of rabies in Alaska was credited with decimating an entire pack of wolves in one instance (Chapman, 1978), and on several occasions a substantial number of wolves wearing radio collars as part of long-term ecological studies have died of rabies (Ritter 1991; Theberge et al., 1994; Kat et al., 1995). Also in Alaska, rabies in a polar bear (*Ursus maritimus*) raised concerns about the potential effects this disease could have on bear populations and the annual

Inuit harvest of this species; concerns were also expressed for human safety when butchering bears potentially infected with rabies (Taylor et al., 1991).

Among the >2,500 cases of rabies in OCMs, only the three cases of rabies identified in lesser pandas (*Ailurus fulgens*) residing in the National Zoological Park, Washington D.C. (Centers for Disease Control and Prevention, 1985), and one case in an ocelot (*Leopardus pardalis*) imported from Peru to California (Frye and Cucuel, 1968) to be kept as a privately owned pet represented disease in true ex-

b Rabies virus variants include Arctic fox, raccoon (Northeast, Mid-Atlantic and Southeast United States [NEngl, MidAtl, SAtl, SCnt]), Southcentral (SC) skunk, Northcentral (NC) skunk, Arizona (AZ) fox, California (CA) skunk, Texas (TX) fox, Mexico (MX) dog, and Puerto Rico mongoose/dog.

^c Not all samples were sequenced to differentiate between TX fox and MX dog, but both variants were identified from these samples.

d Bat species: PH—Pipistrellus hesperus, TB—Tadarida brasiliensis.

otic species for the US. The pandas were infected with the raccoon variant of the rabies virus and thus disease was the result of spillover, probably from raccoons, during residence at the National Zoological Gardens. The ocelot, which was sick upon arrival in California, died within a month. Thus, although the virus variant involved was not identified, infection almost certainly occurred before arrival in the United States. Mongooses, although not native to Puerto Rico, have been present in the Caribbean since the 1870s when they were introduced to control rats in sugar cane fields (Everard and Everard, 1988). Cases of rabies in domestic ferrets also represent disease in a non-native species; however, this animal is also not a recent import and is now classified with dogs and cats as a domestic species for purposes of rabies control (Jenkins et al., 2000). The earliest recorded case of rabies in a ferret reported to CDC dates from 1958 (Centers for Disease Control and Prevention, 1983), and there have been only 23 additional cases reported since then.

Several animals appearing in the table of rabid OCMs deserve mention and special attention, beyond that which would be accorded them because of the frequency with which they are reported rabid. There have been several recent accounts of unprovoked attacks by otters, either singly or in packs of up to five animals, on humans swimming near the animals (T. Baptista, pers. comm.; Breitler, 2001). Instances such as these warrant prompt action to treat the victims for possible rabies exposure. In 1991, a wounded otter that was rescued and cared for by a local veterinary facility in Georgia and home-cared for by multiple persons on weekends subsequently developed rabies, resulting in a multistate search for exposed persons (Serfass et al., 1995). Reports of rabies among otters, although uncommon, increased from five between 1980 and 1989 to 36 between 1990 and 2000. In addition, their geographic distribution encompasses most of North America (Wilson and Reeder, 1993), and rabid otters have been reported from four of the seven regions of the United States.

The range of ringtails is restricted to drier regions of the southwestern states, where their climbing and leaping abilities are legend. Perhaps the agility and nocturnal predatory skills of this species and the general sparsity of terrestrial reservoir species in areas where they occur offer an explanation for the fact that the only two variants of the rabies virus recovered from ringtails were found to be associated with bats.

The first reports of rabies among wolfdog hybrids occurred within the last decade as the popularity and numbers of these animals increased (Siino, 2000). How frequently these hybrids bite humans is unknown; however, wolf-dog hybrids were involved in 14 fatal (non-rabies) human attacks between 1979 and 1998, which places them sixth among all breeds (Sacks et al., 2000). Currently, there is no rabies vaccine licensed for use in wolf-dog hybrids, and in one instance a wolf-dog hybrid vaccinated off-label with a United States Department of Agriculture-approved canine vaccine developed rabies (Jay et al., 1994).

Rabies among OCMs remains primarily a regional problem. Under most circumstances, when spillover to carnivore species not involved as the primary host of a particular rabies virus variant occurs, maintenance remains uncommon. However, this review was intended in part to remind public health professionals that OCMs can be infected by rabies virus, and therefore bites to humans from all wildlife species warrant a careful appraisal for the potential risk of rabies. Antigenic and genetic typing provide valuable mechanisms for detection of new variants of rabies and other exotic lyssaviruses that might be introduced by exotic OCMs and other nonindigenous mammal species.

ACKNOWLEDGMENTS

The authors thank the state and territorial health departments and laboratories for their contributions of rabies surveillance data; M. Smith for his contributions and early organizational work with these data while serving an epidemiology elective with the Viral and Rickettsial Zoonoses Branch, Division of Viral and Rickettsial Diseases, National Center for Infectious Diseases, Centers for Disease Control and Prevention (CDC); and J. O'Connor, Office of the Director, Division of Viral and Rickettsial Diseases, CDC for editing and critical comments.

LITERATURE CITED

- BAER, G. M., AND J. S. SMITH. 1991. Rabies in non-hematophagous bats. *In* The natural history of rabies. G. M. Baer (ed.). CRC Press, Boca Raton, Florida, pp. 341–366.
- Breitler, A. 2001. Otter attacks Lake Shasta swimmer. *In* The Redding Record Searchlight. Redding, California, p. A1.
- Centers for Disease Control and Prevention. 1983. Rabies surveillance annual summary 1980–1982. US Department of Health and Human Services, Atlanta, Georgia.
- ——. 1985. Rabies surveillance annual summary 1983. US Department of Heath and Human Services, Atlanta, Georgia.
- Chapman, R. C. 1978. Rabies: Decimation of a wolf pack in arctic Alaska. Science 201: 365–367.
- CLARK, K. A., S. U. NEILL, J. S. SMITH, P. J. WILSON, V. W. WHADFORD, AND G. W. McKIRAHAN. 1994. Epizootic canine rabies transmitted by coyotes in south Texas. Journal of the American Veterinary Medical Association 204: 536–540.
- CLARK, W. R., AND E. K. FRITZELL. 1992. A review of population dynamics of furbearers. *In* Wildlife 2001: Populations. D. R. McCullough and R. H. Barett (eds.). Elsevier, London, UK, pp. 899– 910.
- Creekmore, T. E., S. B. Linhart, J. L. Corn, M. D. Whitney, B. D. Snyder, and V. F. Nettles. 1994. Field evaluation of baits and baiting strategies for delivering oral vaccine to mongooses in Antigua, West Indies. Journal of Wildlife Diseases 30: 497–505.
- EVERARD, C. O., AND J. D. EVERARD. 1988. Mongoose rabies. Reviews of Infectious Diseases 10 Suppl. 4: S610–S614.
- FARRY, S. C., S. E. HENKE, S. L. BEASOM, AND M. G. FEARNEYHOUGH. 1998. Efficacy of bait distributional strategies to deliver canine rabies vaccines to coyotes in southern Texas. Journal of Wildlife Diseases 34: 23–32.
- FEARNEYHOUGH, M. G., P. J. WILSON, K. A. CLARK, D. R. SMITH, D. H. JOHNSTON, B. N. HICKS, AND G. M. MOORE. 1998. Results of an oral rabies vaccination program for coyotes. Journal of the American Veterinary Medical Association 212: 498–502.

- FRYE, F. L., AND J. P. CUCUEL. 1968. Rabies in an ocelot. Journal of the American Veterinary Medical Association 153: 789–790.
- JAY, M. T., K. F. REILLY, E. E. DEBESS, E. H. HAYNES, D. R. BADER, AND L. R. BARRETT. 1994. Rabies in a vaccinated wolf-dog hybrid. Journal of the American Veterinary Medical Association 205: 1729–1732.
- JENKINS, S. R., M. AUSLANDER, L. CONTI, R. H. JOHNSON, M. J. LESLIE, F. E. SORHAGE, D. J. BRIGGS, J. E. CHILDS, M. CURRIER, N. FRANK, B. WATSON, R. B. MILLER, C. E. RUPPRECHT, AND C. V. TRIMARCHI. 2000. Compendium of animal rabies prevention and control, 2000. Journal of the American Veterinary Medical Association 216: 338–343.
- KAT, P. W., K. A. ALEXANDER, J. S. SMITH, AND L. MUNSON. 1995. Rabies and African wild dogs in Kenya. Proceedings of the Royal Society of London B Biological Sciences 262: 229–233.
- KIMBER, K. R., G. V. KOLLIAS, AND E. J. DUBOVI. 2000. Serologic survey of selected viral agents in recently captured wild North American river otters. Journal of Zoo and Wildlife Medicine 31: 168–175.
- Krebs, J. W., J. S. Smith, C. E. Rupprecht, and J. E. Childs. 2000. Mammalian reservoirs and epidemiology of rabies diagnosed in human beings in the United States, 1981–1998. Annals of the New York Academy of Sciences 916: 345–353.
- ——, A. M. MONDUL, C. E. RUPPRECHT, AND J. E. CHILDS. 2001. Rabies surveillance in the United States during 2000. Journal of the American Veterinary Medical Association 219: 1687–1699.
- LINHART, S. B., T. E. CREEKMORE, J. L. CORN, M. D. WHITNEY, B. D. SNYDER, AND V. F. NETTLES. 1993. Evaluation of baits for oral rabies vaccination of mongooses: Pilot field trials in Antigua, West Indies. Journal of Wildlife Diseases 29: 290–294.
- MACDONALD, D. W. 1993. Rabies and wildlife: A conservation problem? Onderstepoort Journal of Veterinary Research 60: 351–355.
- McQuiston, J. H., P. A. Yager, J. S. Smith, and C. E. Rupprecht. 2001. Epidemiologic characteristics of rabies virus variants in dogs and cats in the United States, 1999. Journal of the American Veterinary Medical Association 218: 1939–1942.
- MOORE, G. C., AND G. R. PARKER. 1992. Colonization by the eastern coyote (Canis latrans). In Ecology and management of the eastern coyote. A. H. Boer (ed.). Wildlife Research Unit, University of New Brunswick, Fredricton, New Brunswick, pp. 21–37.
- Noah, D. L., C. L. Drenzek, J. S. Smith, J. W. Krebs, L. Orciari, J. Shaddock, D. Sanderlin, S. Whitfield, M. Fekadu, J. G. Olson, C. E. Rupprecht, and J. E. Childs. 1998. Epidemiology of human rabies in the United States, 1980

- to 1996. Annals of Internal Medicine 128: 922–930.
- RITTER, D. G. 1991. Rabies in Alaskan furbearers: A review. *In Proceedings of the sixth northern furbearer conference*. Alaska Department of Fish and Game, Fairbanks, Alaska, pp. 26–34.
- ROHDE, R. E., S. U. NEILL, K. A. CLARK, AND J. S. SMITH. 1997. Molecular epidemiology of rabies epizootics in Texas. Clinical Diagnostic Virology 8: 209–217.
- SACKS, J. J., L. SINCLAIR, J. GILCHRIST, G. C. GOLAB, AND R. LOCKWOOD. 2000. Breeds of dogs involved in fatal human attacks in the United States between 1979 and 1998. Journal of the American Veterinary Medical Association 217: 836–840.
- SERFASS, T. L., M. T. WHARY, R. L. PEPER, R. P. BROOKS, T. J. SWIMLEY, W. R. LAWRENCE, AND C. E. RUPPRECHT. 1995. Rabies in a river otter (*Lutra canadensis*) intended for reintroduction. Journal of Wildlife Diseases 26: 311–314.

- SIINO, B. S. 2000. Crossing the line. ASPCSA Animal Watch Winter. 2000: 22–29.
- SMITH, J. S. 1989. Rabies virus epitopic variation: Use in ecologic studies. Advances in Virus Research 36: 215–253.
- , L. A. Orciari, and P. A. Yager. 1995. Molecular epidemiology of rabies in the United States. Seminars in Virology 6: 387–400.
- Taylor, M., B. Elkin, N. Maier, and M. Bradley. 1991. Observation of a polar bear with rabies. Journal of Wildlife Diseases 27: 337–339.
- Theberge, J. B., G. J. Forbes, I. K. Barker, and T. Bollinger. 1994. Rabies in wolves of the Great Lakes region. Journal of Wildlife Diseases 30: 563–566.
- WILSON, D. E., AND D. M. REEDER (Editors). 1993.
 Mammal species of the world, 2nd Edition,
 Smithsonian Institution Press, Washington, D.C.,
 pp. 311.

Received for publication 14 June 2002.