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Source: Journal of Wildlife Diseases, 24(3) : 434-449

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-24.3.434

Journal of Wildlife Diseases, 24(3), 1988, pp. 434–449

RABIES AND RABIES CONTROL IN STRIPED SKUNKS (*MEPHITIS MEPHITIS*) IN THREE PRAIRIE REGIONS OF WESTERN NORTH AMERICA

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ABSTRACT: The number and geographic distribution of rabies cases in striped skunks (*Mephitis mephitis*) from Saskatchewan (n = 2,506 cases), Montana (n = 1,142), and Alberta (n = 199) since 1963 were reviewed. In Saskatchewan the number of cases increased steadily for 5 yr and then fluctuated consistently in a 4 yr cyclic pattern. Similarly an initial sweep across the province was followed by a cyclic pattern of geographic expansion (3 to 4 yr) and reduction (1 to 2 yr). No organized control efforts were conducted in Saskatchewan. Similar cyclic patterns were not seen in data from Montana or Alberta. In the latter areas, the number and distribution of rabies cases in skunks appeared to reflect efforts to reduce the population of skunks. An integrated program of skunk removal using poison and live-traps in association with research and public education successfully contributed to limiting the spread and establishment of rabies in striped skunks within prairie habitats. Rabies did not persist in skunks in other habitats.
Key words: Rabies, striped skunk, review, prairies, rabies control, *Mephitis mephitis*.

INTRODUCTION

During the 1950's, a consistent pattern emerged as rabies virus became established in the Great Plains region of central North America (Parker, 1975). The outbreak appeared geographically and ecologically distinct from rabies in other areas. It continued to spread westward and by 1959 included North and South Dakota (USA) and southern Manitoba (Canada) (Verts, 1967; Tabel et al., 1974). Nearly all wildlife cases involved striped skunks (*Mephitis mephitis*). Rabies in spotted skunks, *Spilogale* spp., rarely was reported (Parker, 1962).

Recent analyses using monoclonal antibodies indicate a single source of virus became established and spread throughout skunks in the northern prairie region (Centers for Disease Control, 1985). This strain of the virus differs from that obtained from other host species or geographic areas tested to date (Smith et al., 1984; CDC, 1985). The current paper focused on three political jurisdictions (Saskatchewan and Alberta, Canada and Montana, USA) to provide a review of rabies in striped skunks in the northwestern prairie regions in North America. Rabies has not been reported in spotted skunks from these areas.

In general, there are three modern approaches to rabies control programs in wildlife in North America: (1) accept the presence of rabies virus in wildlife populations and rely on an immune barrier accomplished by vaccination of the domestic pet population, public education programs, and the awareness of medical and veterinary professions to reduce the impacts of the disease; (2) vaccinate specific free-ranging wildlife species to reduce the prevalence of rabies infection (Steck and Wandler, 1980; Tinline et al., 1982; Anderson, 1986; Blancou et al., 1986); or (3) reduce the number of individuals in free-ranging populations, thus reducing the rate of transmission and the availability of infected and uninfected hosts (Lewis, 1975; Macdonald, 1980; Rosatte et al., 1986). Repeated attempts to control the disease in free-ranging, mobile host species have achieved differing levels of success (as reviewed in Lewis, 1975; Macdonald, 1980; Macdonald and Voigt, 1985). Rabies control efforts differed substantially in Saskatchewan, Montana and Alberta. Popu-

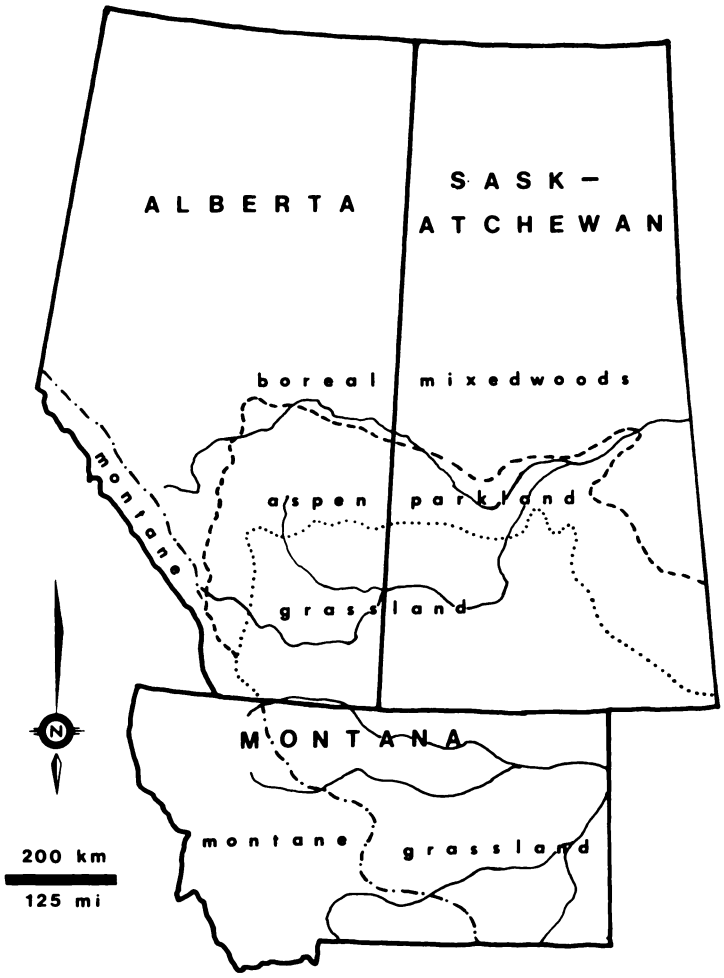

FIGURE 1. Major ecoregions in Saskatchewan and Alberta, Canada and Montana, USA. Important river systems are indicated.

lation reduction as a long-term method of controlling rabies in a prairie habitat was evaluated using the information gathered during the current review.

There are inherent difficulties in evaluating data collected through diagnostic laboratories (Lewis, 1972; Constantine et al., 1979; Macdonald, 1980). Although the influences of sample bias and incomplete reporting cannot be avoided, they are most noticeable in evaluation of small sample periods (Snedecor and Cochran, 1967). The current review attempted to minimize these errors by considering data collected over a long period (23 yr) and three large geographic areas. A comparison of patterns and trends in the rabies data within and between these areas is provided.

Background information

The known range of striped skunks includes all of Saskatchewan, Montana and Alberta (Banfield, 1974). These areas provide a variety of habitat types suitable for skunks (Mueggler and Stewart, 1980; Strong and Leggat, 1981). They are, in part, within the northern limit of the Great Plains region of North America which is characterized by grassland areas including short-grass, mixed grass and fescue grass ecoregions (Fig. 1). In Saskatchewan and Alberta a narrow band of aspen parkland

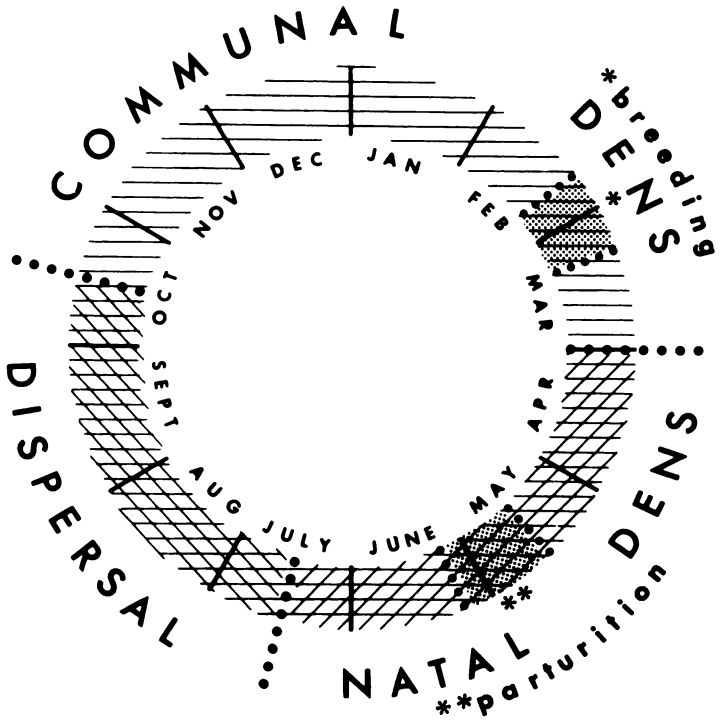

FIGURE 2. A generalized life history of striped skunks in northwestern North America.

separates the grasslands from a broad expanse of northern boreal forest. In Montana and Alberta, montane and subalpine ecoregions provide the western boundary of the grasslands. The grasslands are a vast area of contiguous vegetation, climate and soil separated only by political boundaries.

Within these three political regions, the human population density, occupation and land use patterns are similar. Human activities are distributed sparsely in the parkland and prairie regions with extensive areas under heavy cereal crop development or livestock husbandry. These areas are interspersed with uncultivated dryland coulees and shallow, often intermittent, sloughs.

The behavior, activity and life history of striped skunks in the prairie and parkland habitats are similar throughout the region (Seyler and Niemeyer, 1974; Gunson and Bjorge, 1979; Andersen, 1981; Bjorge et al., 1981; Schowalter and Gunson, 1982; Rosatte and Gunson, 1984); its life history is summarized in Figure 2. Activity of skunks is focused around occupied or abandoned building sites, farmsteads, culverts, coulees and rockpiles. Adults are relatively sedentary, utilizing small home ranges and travelling minimal distances during the year (Andersen, 1981; Bjorge et al., 1981). Population turnover is rapid with approximately 45% of the population as juveniles and 34% as yearlings; only 5% of adult males and 8% of adult females were >3 yr old (Schowalter and Gunson, 1982).

MATERIALS AND METHODS

Records concerning diagnosed cases of rabies in Saskatchewan and Alberta were received from Agriculture Canada (Nepean, Ontario, K2H 8P9, Canada) and, in Montana, Montana Department of Livestock (Helena, Montana 59620, USA). They were summarized on an annual calendar basis. Skunks tested for rabies were submitted by the public or by rabies control personnel. In all cases the fluorescent antibody test (Beauregard et al., 1965) was conducted.

The annual number of cases reported and the prevalence (percent infected after the definition of Margolis et al., 1982) of rabies in striped

skunks were determined where possible. Additional data were gleaned from previous literature reports. The annual geographic distribution of diagnosed cases was mapped using land location (Saskatchewan and Alberta) or county (Montana). Details concerning rabies control efforts were summarized from the files of Saskatchewan Department of Agriculture (Regina, Saskatchewan, Canada S4S 0B1), Montana Department of Livestock, and Alberta Fish and Wildlife Division (Edmonton, Alberta, Canada T6H 4P2).

RESULTS

Saskatchewan, Canada

Rabies was first identified in skunks in Saskatchewan in 1963 (Hayles and Dryden, 1970). The annual number of reported cases increased gradually between 1963 and 1968. Subsequently the pattern of annual cases appeared cyclic on a 4 to 5 yr basis (Table 1, Fig. 3). Peak values were followed by a rapid decline within 1 or 2 yr. The pattern of annual cases indicated a gradual peak and decline during the first 10 yr, followed by three consistent cyclic periods varying between 100 and 200 cases annually in the next 10 yr. The number of cases increased markedly in 1986 (395 cases, a 93% increase over 1985). Most cases (77%) were in grassland habitats (Table 2).

The prevalence of rabies in skunks submitted by the public in Saskatchewan decreased from 92% (12 of 13) in 1964 to 39% (67 of 171) in 1968 and in domestic species decreased from 53% (17 of 32) to 9% (21 of 235) (Hayles and Dryden, 1970). Gunson et al. (1978) reported a prevalence of 52% in 1,281 skunks submitted by the public between 1970 and 1976. The annual prevalence remained at similar levels after that time ($\bar{x}_5 = 47\% \pm 6$, 1981 to 1985, $n = 1{,}684$). Between 1972 and 1976, the prevalence in 431 skunks collected during random surveys in Saskatchewan was 3% (Gunson et al., 1978).

Rabies in skunks was diagnosed initially in southeastern Saskatchewan but spread rapidly westward and approached the border with Alberta by 1971. The geographic area of infection reached a maximum in 1968 (Hayles and Dryden, 1970) and then withdrew to the central region of the province between 1969 and 1971 (Fig. 4a). Isolated cases were identified peripheral to the main area during this period. Between 1972 and 1975 the area of infection expanded gradually throughout southern regions (Fig. 4b). After 1972, rabies was not diagnosed along the northern portion of

TABLE 1. Rabies cases diagnosed in three prairie regions, 1963–1986.

	Saskatchewan		Montana		Alberta	
	Skunks	Total cases	Skunks	Total cases	Skunks	Total cases
1963	1	1	0	1	0	0
1964	12	24	5	8	0	0
1965	15	32	2	4	0	1
1966	25	46	15	15	0	1
1967	44	54	3	11	0	0
1968	67	90	7	12	0	0
1969	25	49	4	4	0	0
1970	28	61	1	3	0	16
1971	1	21	1	4	1	21
1972	44	63	5	7	3	12
1973	215	268	38	44	6	42
1974	100	123	44	49	7	28
1975	95	118	152	172	3	25
1976	142	163	73	92	4	32
1977	188	208	38	56	4	12
1978	102	122	15	26	0	5
1979	69	93	7	21	3	15
1980	99	115	36	56	54	66
1981	202	225	72	123	23	33
1982	112	128	56	97	43	51
1983	128	137	94	119	32	40
1984	162	185	101	128	7	13
1985	205	231	207	253	8	12
1986	395	439	166	205	1	6

TABLE 2. Frequency of occurrence (%) of rabies in striped skunks in various habitat types, 1963–1986.

	Saskatchewan	Montana	Alberta
Total cases	2,506	1,142	199
Grassland	77.4	95.3	97.0
Parkland	21.8	—	2.5
Montane	—	0.6	0
Other	0.8[a]	4.1[b]	0.5[a]

[a] Boreal mixedwoods.
[b] Grassland/montane.

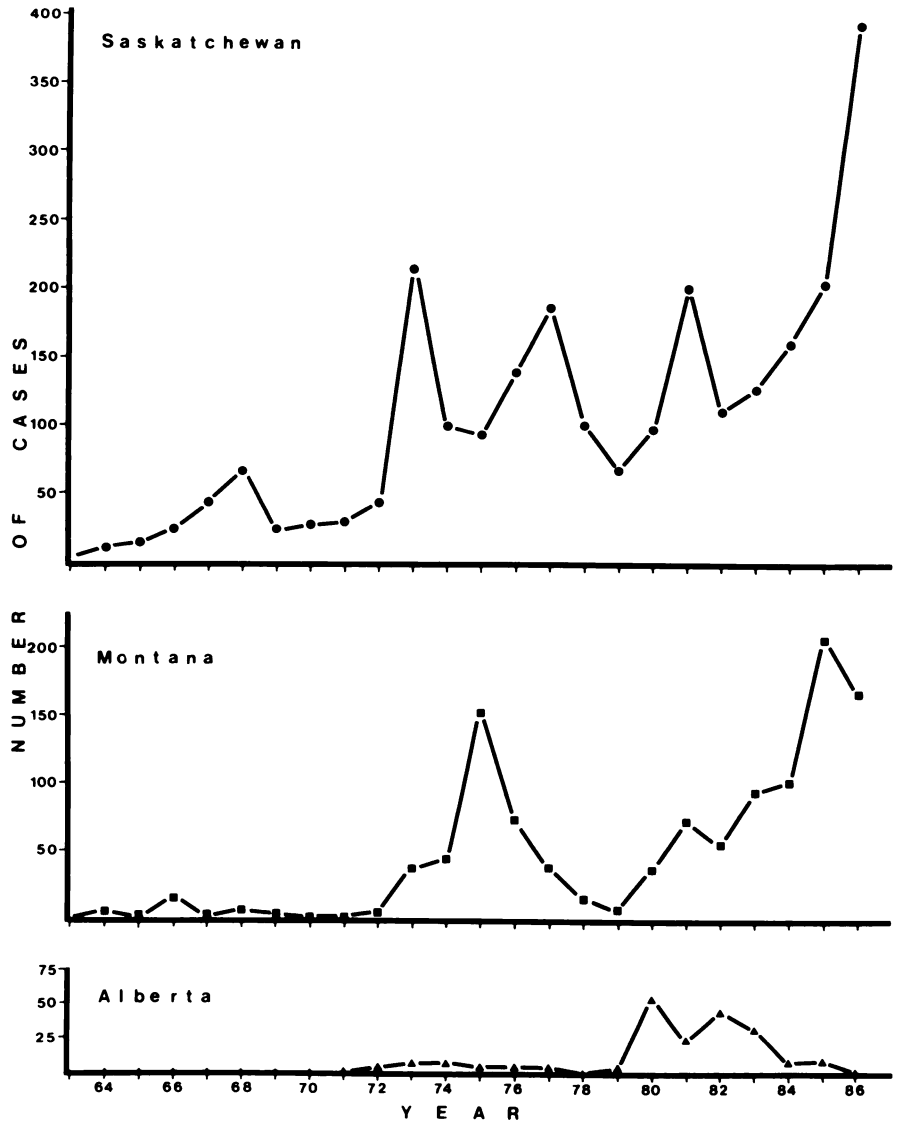

FIGURE 3. Annual incidence of rabies in striped skunks in three prairie regions of North America.

the Alberta and Saskatchewan border and only one case was reported in the area between the North and South Saskatchewan rivers. The disease reached its maximum distribution in 1977 (Fig. 4c) but had already started to withdraw from southwestern Saskatchewan. Cases were reported as far north as Prince Albert but only one case was in the area between the rivers.

In the late 1970's, the geographic area of reported rabies cases continued to withdraw and by 1980 most cases were reported from the southeastern corner of Saskatchewan (Fig. 4d). In 1981 rabies expanded rapidly throughout central and eastern Saskatchewan and was reported in an area similar to that in 1977. However, the disease quickly withdrew in 1982 and the area affected was reduced to three disjunct regions by 1983 (Fig. 4e). The disease increased once again and by 1986 was reported from most of southern and central Saskatchewan (Fig. 4f).

During the 1960's, efforts to control ra-

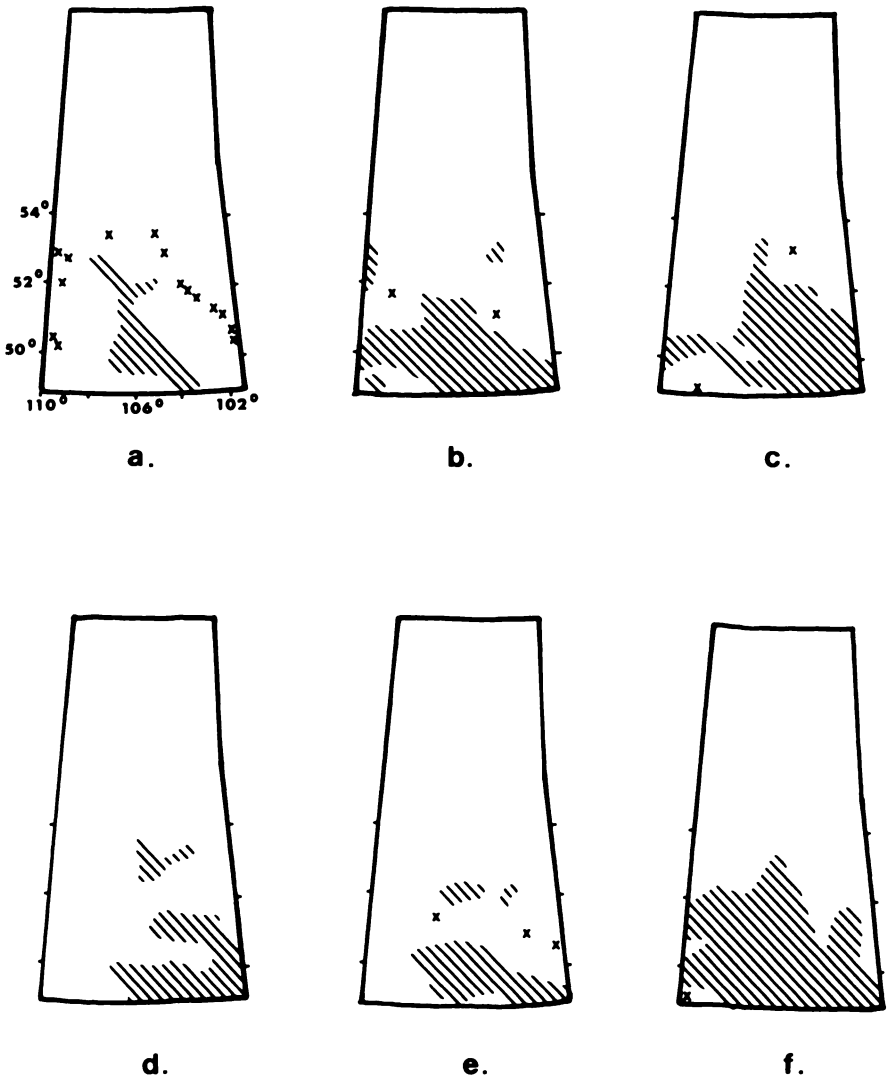

FIGURE 4. Geographic distribution of rabies diagnosed in striped skunks in Saskatchewan (▨—area reporting rabies cases, x = single cases). 4a. 1969 to 1971. 4b. 1972 to 1975. 4c. 1977. 4d. 1980. 4e. 1983. 4f. 1986.

bies in skunks in Saskatchewan focused on public, veterinary and medical awareness of skunks and rabies. Specific programs to reduce the number of skunks were considered too costly and labour-intensive. Although landowners in southeastern Saskatchewan were encouraged to use smoke bombs (11% sulphur) to kill skunks in dens, very few were used. During the early 1970's, conservation officers placed a limited number of poison eggs (1.5 cc of 2% strychnine per egg) and smoke bombs in areas of known skunk activity. The program was not coordinated among areas and had little effect. Control efforts continued to rely heavily on the public to remove skunks, but the number of skunks removed was minimal.

Following a resurgence of rabies cases in 1985 and 1986, a need for increased public awareness and an organized skunk control program in Saskatchewan was identified (Harvey, 1987). However, the program continued to rely on prevention

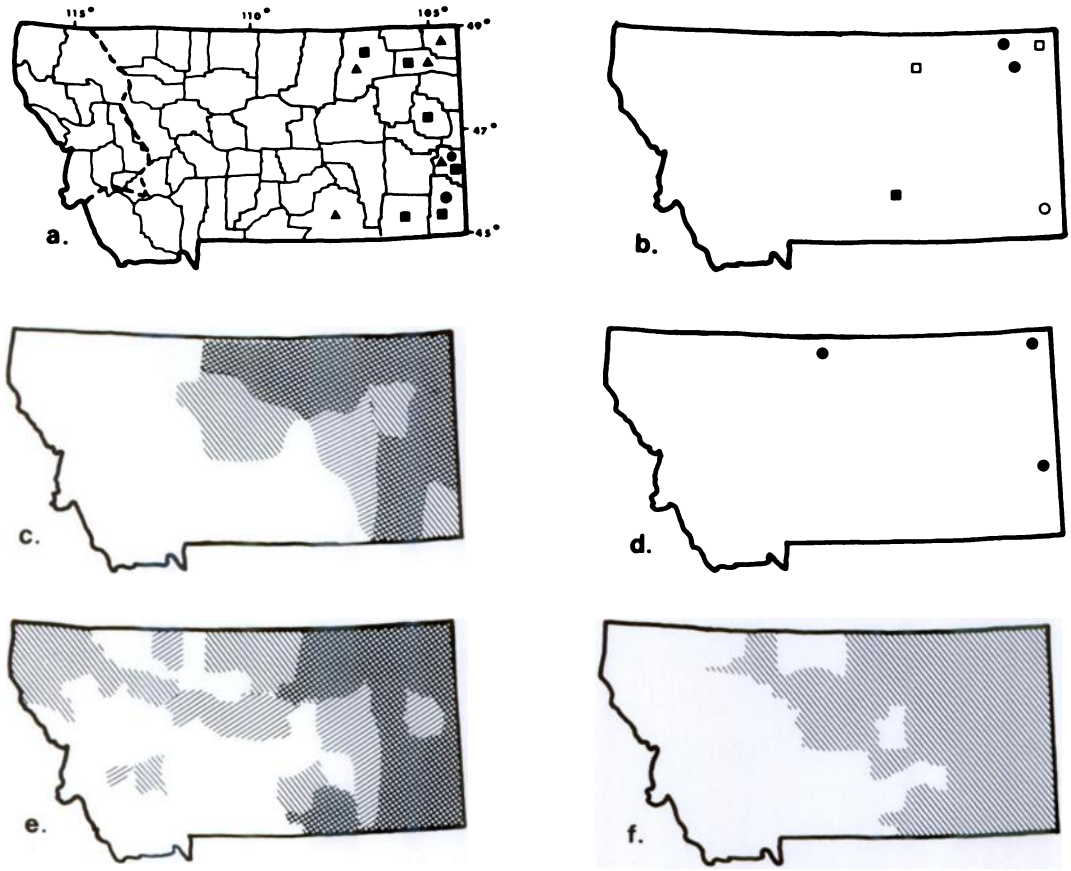

FIGURE 5. Geographic distribution of rabies diagnosed in striped skunks in Montana. 5a. 1964 to 1968 (●—1964, □—1966, ▲—1968). 5b. 1969 to 1972 (●—1969, ○—1970, ■—1971, □—1972). 5c. 1974 to 1977 (▨—1974, ▧—1977). 5d. 1979. 5e. 1980 to 1983 (▧—1981, ▨—1983). 5f. 1986.

of rabies through (1) vaccination of pets, (2) vaccination of high risk humans, (3) reporting of suspect animals, and (4) rabid skunk control (coordinated by rural municipalities on a voluntary basis but conducted largely by the public) (Harvey, 1987). Organized removal of skunks was not implemented.

In summary, the pattern of rabies in skunks in Saskatchewan indicated a gradual increase in the number of cases as the disease spread in a diffuse pattern radiating in all directions from an advancing front (Hayles and Dryden, 1970). The disease appeared as a broad advancing band preceded by a fringe of isolated cases and followed by a lower number of cases distributed over a large area. Recurrent waves of prolonged geographic expansion (3 to 4 yr) followed by rapid reduction (1 to 2 yr) swept back and forth across the southern and central parts of the province. Maximum expansion of the disease usually coincided with a peak number of cases. The disease moved quickly within the short grass and mixed prairie ecoregions but invaded slowly and did not persist within the aspen parkland. The North and South Saskatchewan rivers may have provided significant geographic barriers but were effectively breached in 1985.

Efforts to limit the spread of the virus by local depopulation of skunks were minimal. These efforts were characterized by a lack of coordination and heavy reliance on public involvement on a voluntary basis. The program was unsuccessful and a general lack of awareness about skunks and

rabies was identified as the primary problem currently hampering rabies control efforts (Harvey, 1987).

Saskatchewan has recorded two human fatalities due to rabies (in 1925 and 1970) and recent reports indicated approximately six people per 100,000 residents receive rabies postexposure treatment annually (Varughese, 1985). Approximately one of every two skunks submitted annually by the public was diagnosed rabid. Rabies remains a significant problem in Saskatchewan.

Montana, USA

Rabies was first diagnosed in striped skunks in Montana in 1964 (Seyler and Niemeyer, 1974) and the annual number of cases remained low ($\bar{x}_9 = 5 \pm 4$ cases) between 1964 and 1972 (Table 1, Fig. 3). The number peaked in 1975 (152 cases) then declined slowly through 1979 (7 cases). After 1979 the number of cases increased steadily. A marked increase was recorded in 1985 (205% of the 1984 total); however, the level decreased slightly in 1986. The majority of cases were in grassland areas (Table 2).

A total of 416 skunks was submitted for rabies diagnosis between 1964 and 1972. The annual prevalence was 12% ± 8 (range 3 to 20). Between 1973 and 1978 the annual prevalence was 20% ± 8 (range 7 to 31, $n = 2{,}072$ skunks) and was significantly higher than in the earlier period ($\chi^2 = 5.11$, $P < 0.05$). More recently the prevalence increased steadily to 57% in 1986.

Rabies in striped skunks in Montana first appeared in the southeast along the border with North Dakota (Seyler and Niemeyer, 1974). Between 1964 and 1968 the area of infection included most of the counties bordering on North and South Dakota (Fig. 5a); however, the number of cases diagnosed was low and the distribution was disjunct between years. By 1972, four of five reported cases were in the extreme northeast (Fig. 5b). An epizootic started in 1973 and within 2 yr included much of eastern and northcentral Montana (Fig. 5c). During this period rabies was diagnosed in the region between the Missouri and Yellowstone rivers for the first time. In 1975 rabies withdrew in the south but expanded westward in the north. The geographic distribution of cases remained relatively stable between 1975 and 1977.

Following a rapid withdrawal in 1978, the disease was reported in only three disjunct counties in 1979 (Fig. 5d). The geographic area of infection moved slowly across the northern part of the state and by 1981 included a few cases west of the Continental Divide (Fig. 5e). Between 1981 and 1983 the infection was widespread but inconsistent among counties. Persistent infection was maintained only in eastern Montana. Rabies was not reported beyond the Divide after 1983. Between 1984 and 1986 the area of infection remained relatively constant with the majority of cases located in the eastern half of the state (Fig. 5f).

In 1966, Montana established a Rabies Control Advisory Committee with representation from various federal and state agencies. The goals outlined by the committee included local containment of rabies in skunks, vaccination of household pets and education of the public. Most skunks were removed with toxicants, primarily strychnine in chicken eggs (1 cc of 3.5 g strychnine in 10% glacial acetic acid) (Seyler and Niemeyer, 1974). Initially, baits of strychnine in fat also were used. Poison eggs or fat were distributed under strict guidelines (Nesse and Seyler, 1976) and could be placed only with approval of the landholder. Toxicant was placed in skunk habitat within 5 km of any skunks diagnosed rabid; however, sites occupied by humans were avoided. Public acceptance of the program was good and cooperation was high.

In 1966 a buffer zone was established along the watershed divide in southeastern Montana. The zone was 3 to 8 km wide and approximately 225 km long extending from the Yellowstone River to the Wyoming border. Strychnine baits were dis-

TABLE 3. Documented rabies control efforts in Montana, 1973–1986.

	Number of eggs[a] placed	Number of skunks collected	Number of eggs per skunk collected	Other species	Source
June 1973–October 1973	3,947	264	15	31	Seyler and Niemeyer, 1974
June 1974	1,379	183	7.5	—	EPA summary
January 1975–July 1975	1,781	309	5.8	26	Nesse and Seyler, 1976
1981–1985					
Total	6,225	2,118	2.9	78[b]	Ferlicka, unpubl. data
Annual average	1,245 ± 439	424 ± 217	3.2 ± 0.5	15 ± 7	Ferlicka, unpubl. data
1986	2,284	945	2.4	108[c]	Ferlicka, unpubl. data

[a] 35 mg strychnine per egg.
[b] Includes 24 raccoons, 23 mice, and 13 foxes.
[c] Includes 43 mice, 38 ground squirrels, and 22 raccoons.

tributed in skunk habitat throughout the buffer zone.

The State of Montana adopted a formal Skunk Rabies Control Policy in January 1975 (Nesse and Seyler, 1976) giving official sanction to the 5 km radial skunk removal programs. Surveillance programs to monitor the presence and spread of rabies in skunks beyond the 5 km limit as well as information and education programs concerning skunks and rabies were included in the policy.

Skunk reduction programs in Montana relied on trapping and shooting after the federal ban in 1972 on the use of toxicants throughout the United States (Nesse and Seyler, 1976). However, state officials considered these methods inefficient, costly and ineffective to deal with the widespread rabies problem. In June 1973, Montana was granted approval to use strychnine for emergency skunk removal (Nesse and Seyler, 1976). However, annual approval from the Environmental Protection Agency was required and in March 1975 the state requested long-term registration of strychnine for use in rabies control programs. The request was granted in June 1987.

Although annual exemption from the ban on toxicants was granted each year from 1973 to 1986, the program often was curtailed pending renewal of authorization. In some years efforts were conducted for only 2 or 3 mo. In addition, toxicants were not used extensively during cold weather. After 1978, radial population reduction around diagnosed cases was incomplete and intermittent. Skunk removal usually was focused at sites uninhabited by humans.

Specific results of the removal programs in Montana often were undocumented. The buffer zone initiated in 1966 was ineffectual and soon discontinued. Data were received for 15,616 poison eggs used throughout the state between June 1973 and December 1986 (Table 3). The number of skunks collected annually increased during this time while the number of eggs used per skunk collected decreased. Results of scent post surveys suggested local populations of skunks declined after a poison program (Seyler and Niemeyer, 1974). Between April 1974 and July 1976, 22% of 1,058 skunks collected during surveillance programs in 22 eastern counties were rabid. In 1975, 16% of 142 skunks collected in the surveillance areas were rabid (Nesse and Seyler, 1976).

In summary, for 10 yr the number of rabies cases in skunks in Montana remained low and the geographic distribution restricted to isolated areas. Subsequently, the pattern of number and distribution of cases was characterized by

two periods of gradual increase and wide distribution separated by a period of prolonged decrease and limited distribution.

Organized efforts to control rabies in skunks were initiated soon after the virus was identified in the state and a high level of public awareness and cooperation was maintained. State and municipal personnel used toxicants extensively to kill skunks within habitats adjacent to all diagnosed cases. Following the federal ban on toxicants, control efforts were severely restricted and the number and geographic distribution of rabies cases in skunks gradually increased. Improved surveillance and removal efforts were reflected in the gradual decline in number and distribution of cases. However, intermittent and inconsistent control efforts were associated with a steady increase in number and wide distribution of cases.

During the 1970's approximately one of each five skunks submitted for diagnostic testing was rabid. More recently rabies was present in one of each two skunks submitted. The disease is recognized as a significant threat to public health and the livestock industry in Montana. The state currently is trying to re-establish consistent and organized population reduction programs to reduce the number of skunks in rabies enzootic areas.

Alberta, Canada

Between 1959 and 1969, rabies was diagnosed in two domestic animals in Alberta; however, no wildlife cases were reported. The disease was first reported in striped skunks in Alberta in 1971 (Gunson et al., 1978) and the number of cases remained low ($\bar{x}_9 = 3 \pm 2$ cases) up to 1980 (Table 1, Fig. 3). An increase in 1980 (maximum 54 cases) was followed immediately by a decline and a gradual reduction in the number of cases. The mean annual number of cases was similar before 1980 and after 1984 ($t = 0.48$, df = 11, $P > 0.05$) but was significantly higher during 1980 to 1984 than all other years ($t = 5.87$, df = 3, $P < 0.05$). Cases were restricted largely to grassland areas (Table 2).

Data concerning the prevalence of rabies in skunks in Alberta were separated as skunks submitted by the public (suspect skunks) and skunks collected "randomly" by control personnel during rabies control programs (survey skunks). Between 1970 and 1976, the prevalence was 3% in 487 suspect skunks collected throughout Alberta (Gunson et al., 1978) and 6% in 253 suspect skunks collected between 1979 and 1985 in southern Alberta (including the rabies enzootic areas). Rabies was diagnosed in 1% of 480 survey skunks collected along the Alberta and Saskatchewan border and <1% in 532 survey skunks collected elsewhere in Alberta (Gunson et al., 1978). Rabies was not identified in 153 survey skunks collected in the border region between 1979 and 1982. The prevalence was 5% in 1,724 and 1% in 2,938 survey skunks collected within the rabies enzootic areas in southern Alberta during 1980 to 1982 and 1983 to 1986, respectively. However, the prevalence differed among regions and years (Rosatte et al., 1986).

Rabies in striped skunks in Alberta was first diagnosed along the border with Saskatchewan. Between 1972 and 1977, the cases were focused in three disjunct areas along the eastern border (Fig. 6). Rabies did not persist in these areas. In December 1979, an epizootic of rabies in two counties (total area approximately 7,000 km^2) in southern Alberta was identified (Rosatte et al., 1986). Between 1979 and 1986, the geographic area of reported cases decreased and became localized within small areas (M. J. Pybus, unpubl. data). An intense local epizootic was reported in 1982 and 1983 within an area of approximately 300 km^2 in one county in southcentral Alberta (Fig. 6). One or two cases were reported annually in this area after 1983.

Since 1971, Alberta has implemented extensive programs to limit the establishment and spread of rabies in skunks within the province. In addition, programs in-

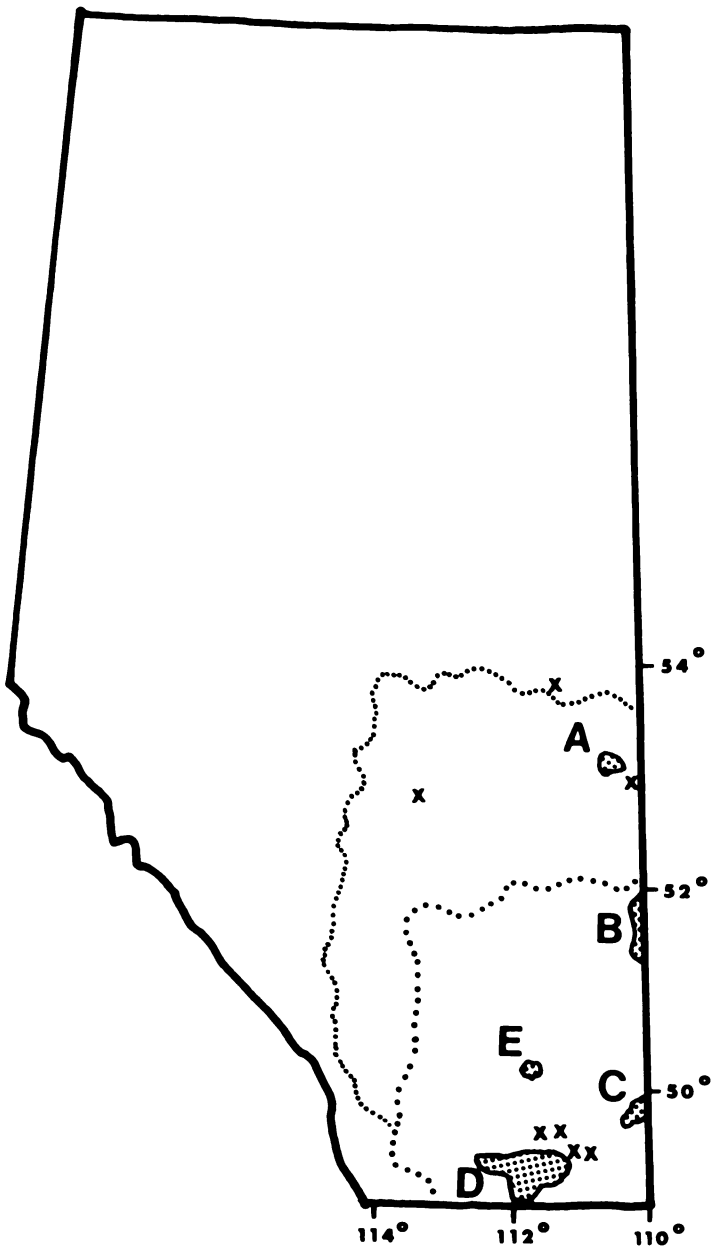

FIGURE 6. Geographic distribution of rabies diagnosed in striped skunks in Alberta (A—1974 to 1977, $r = 3$ cases; B—1972 to 1974, $n = 3$; C—1973 to 1977, $n = 11$; D—1979 to 1985, $n = 129$; E—1982 to 1986, $n = 37$; x—single cases.)

vestigating the biology of skunks in parkland and prairie habitats, and providing public awareness and education about skunks and rabies were conducted. Population reduction programs were undertaken in a corridor along the border with Saskatchewan (1971 to 1986) and within three counties in southern Alberta (1980 to 1986). All programs were cooperative projects involving various federal, provincial, and municipal agencies and were under the direction of Alberta Agriculture (Edmonton, Alberta, Canada T6H 5T6). Details of these programs were presented

previously (Gunson et al., 1978; Rosatte et al., 1986; Pybus, 1987). Population reduction was achieved through an integrated program of live-trapping (wire box traps baited with sardines), or poisoning with strychnine in chicken eggs (1.0 to 1.5 cc of 3% strychnine in 10% glacial acetic acid per egg) or tallow baits (30 to 35 mg strychnine per bait). Additional skunks were taken by shooting, kill-trapping (Conibear 110 or 120 traps, Woodstream Corporation, Lititz, Pennsylvania 17543, USA), or gassing with carbon monoxide.

Eggs or traps were placed throughout appropriate skunk habitat within 5 km of each rabid skunk. This area was expanded as more rabid skunks were identified. In addition, skunks were collected during night-lighting surveys throughout the border region (Gunson et al., 1978) and in trapping and poisoning programs in areas adjacent to the enzootic areas (Rosatte et al., 1986). At least 4,249 and 4,662 skunks were removed in survey programs along the border and in southern Alberta, respectively. Undoubtedly, additional animals were killed but not recovered or were not submitted for rabies testing.

In summary, the number and geographic distribution of rabies cases in skunks in Alberta over the 23-yr period was restricted to a few cases found in small local areas within the grassland and parkland regions. A coordinated program of population reduction targeted against skunks was implemented as soon as the disease was identified on the eastern border. Efforts relied on an integrated program of trapping and poisoning to reduce the number of skunks throughout buffer zone areas or within all areas adjacent to known rabies cases. Considerable research effort provided background knowledge and understanding of the biology of skunks in prairie and parkland habitats. Thus, the efficiency, evaluation and cost-efficiency of removal programs were improved. The programs were maintained with consistent effort on a long-term basis.

Control programs appeared to contribute significantly to limiting the establishment of rabies in skunks in Alberta. Approximately one of each 20 skunks submitted annually by the public was rabid. Although the first human rabies fatality in Alberta was recorded recently (McLean, 1985), the per capita postexposure rate in 1984 (2.1 people per 100,000 residents) was low (Varughese, 1985). Alberta continues to implement the control programs wherever the disease is identified in terrestrial species.

DISCUSSION

The cyclic pattern of rabies in skunks in Saskatchewan is similar to the general epizootiological pattern following the invasion of a pathogenic microparasite into a naive susceptible population (Mollison, 1977; May and Anderson, 1979; Anderson and May, 1986). The consistency of the pattern suggests that the minimal control efforts in Saskatchewan had little or no effect on the spread of the disease. Oscillating patterns of "troughs" and "epizootics" are present in many microparasitic infections of vertebrates (Anderson and May, 1986) and cyclic patterns have been described for rabies in species other than skunks (Preston, 1973; Carey et al., 1978; Macdonald, 1980; Voigt and Tinline, 1982).

The number of cases and geographic distribution of rabies in red foxes in Ontario (Canada) fluctuates at intervals of 3 to 5 yr but the pattern is not observed consistently in skunks in the same area (Macdonald and Voigt, 1985). The epizootiology of rabies in an area where skunks are the only major terrestrial host (that is, in a prairie region) has not been examined previously on a long-term basis.

Within a local population, there may be three phases within the cyclic fluctuation in the number and geographic distribution of reported cases (Fig. 7; adapted from Macdonald, 1980). Initial invasion is associated with an epizootic outbreak as a large number of susceptible individuals are infected. As the disease front passes through the local population, the epizootic is fol-

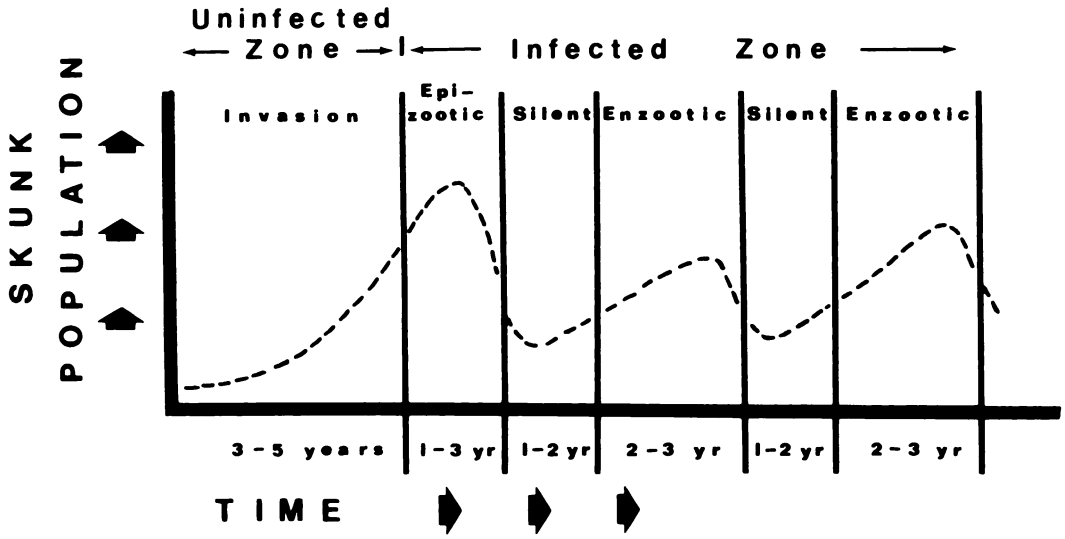

FIGURE 7. Hypothetical fluctuations in the number and geographic distribution of rabies cases in a local population of skunks in a prairie region (adapted from Macdonald, 1980).

lowed by a silent phase with few cases reported. This, in turn, is replaced by an enzootic phase as the number of cases increases again. The silent and enzootic phases are repeated with time. Over a broad area these latter phases are reflected in recurrent expansion and reduction of the geographic area of the reported cases. The pattern in skunks, as exemplified by the Saskatchewan data, appeared to involve a 3 to 4 yr invasion period, 2 to 3 yr epizootic phase, and successive silent (1 to 3 yr) and enzootic (2 to 3 yr) phases. Recurrent peaks were 4 yr apart.

The driving mechanisms behind the oscillations are unknown. May and Anderson (1979) suggest that cyclic patterns in disease outbreaks may be derived from stochastic fluctuations at low prevalence levels, seasonal fluctuations in transmission, or non-linear variation in population parameters. The current oscillations appear to reflect the natural population dynamics of striped skunks in a prairie habitat. In this habitat, few skunks live beyond 3 yr and most are juveniles or yearlings (Schowalter and Gunson, 1982). Fluctuations in the number of skunks in undisturbed populations (Allen and Shapton, 1942; Verts, 1967; Bjorge et al., 1981) occur rapidly and may oscillate on a short time scale. The abundance of suitable habitat or food are not limiting factors for skunks in Saskatchewan (Hayles and Dryden, 1970; Andersen, 1981). Although catastrophic mortality occurs in local populations (Bjorge et al., 1981) it tends to be erratic and unpredictable. In general, skunks are well-adapted to the seasonal aspects of survival in a north temperate climate (Verts, 1967; Aleksiuk and Stewart, 1977; Mutch and Aleksiuk, 1977). In the absence of control programs, rabies may be the major factor in the cyclic regulation of skunk populations in Saskatchewan. Rabies control activities in Montana and Alberta appeared to disrupt the pattern.

The availability of habitat suitable for skunks and the distribution, behavior, and abundance of skunks appears similar in all three prairie regions (Nesse and Seyler, 1976; Gunson and Bjorge, 1979; Andersen, 1981). Public awareness and vaccination of pets was promoted by medical and veterinary agencies in each region. However the epizootiology of rabies in skunks differed markedly among Saskatchewan, Montana and Alberta. The only consistent difference among these regions was the extent of rabies control.

Efforts to control infectious diseases may be affected by a variety of factors (for example, geographic barriers, natural mortality and intrinsic limitations within host and parasite populations) (Fine et al., 1982). Reducing the host population also may affect the outcome of such efforts. Data examined in this review suggested a correlation between the spread of rabies and the extent of population reduction; when control efforts occurred, rabies decreased.

Saskatchewan did not implement organized skunk removal programs within the province and the virus established widespread distribution in skunk populations within 5 yr. Montana initially implemented population reduction programs and nearly 10 yr after invasion, rabies remained restricted to small local areas and a few isolated cases. However, when control efforts became intermittent and inconsistent, the disease spread and established in skunks throughout the state. In contrast, Alberta actively maintained consistent population reduction programs throughout the 15-yr period following identification of rabies in skunks in the province. The disease in Alberta remained isolated in small areas with very few cases reported. Previous efforts have indicated that population reduction is a feasible method to help control rabies in Alberta (Ballantyne, 1958; Gunson et al., 1978; Rosatte et al., 1986).

Attempts to provide computer simulation of rabies epizootiology indicate that control efforts can markedly affect the pattern of disease infection over broad areas (Preston, 1973; Frerichs and Prawda, 1975; Carey et al., 1978; Anderson et al., 1981; Voigt et al., 1985). Current data provide field evidence to support this conclusion as it relates to rabies in a prairie habitat. However, successful control appeared to be associated with integrated field programs of population reduction combined with related research and public education. Efforts must be consistent and maintained on a long-term commitment.

The epizootiology of rabies in the prairies differs from that in other habitat types in North America. The striped skunk is the only terrestrial host required to maintain a viable population of the virus and the biology of this host is unique as a vector of rabies. Skunks are sedentary animals exhibiting minimal dispersal or migration. Their activity in a grassland region is focused at building sites and areas of human activity (rockpiles, fencerows, irrigation ditches, culverts) since they avoid expansive fields under cereal crop cultivation. Thus, optimum habitat is distributed sparsely (but often is accessible by roads or trails). Dramatic relief associated with sandstone bluffs and broad meandering rivers appear to be significant barriers to movement of skunks. Skunks in the parkland and northern prairie regions exhibit long periods of inactivity in communal winter dens with an average of six other skunks. These features of the life history suggest transmission of rabies may be localized in small pockets within the general habitat type. As a result, the disease moves slowly through local populations of skunks. Within 2 or 3 yr, recruitment of young skunks is sufficient to provide a new generation of susceptible individuals and an associated increase in transmission and peak in the number of rabies cases.

In a prairie habitat, it appears that population reduction can play an important role in helping to limit the spread of rabies. The apparent success in the area examined may be associated with the unique aspects of the disease in this habitat (as indicated above). Efforts can be focused on a single accessible host species and concentrated temporally and spatially to enhance their effectiveness. Wildlife managers should be aware of the potential of population reduction to help control rabies in the prairie region.

ACKNOWLEDGMENTS

Various people gave freely their time and access to their records during preparation of this review. The author gratefully acknowledges the cooperation and assistance of M. Dorrance (Al-

berta Agriculture), D. Harvey (Saskatchewan Agriculture), D. Gregory (Agriculture Canada, Nepean), O. James and D. Ferlicka (Montana Department of Livestock), P. Varughese (Health and Welfare Canada), J. Waters (Alberta Community and Occupational Health) and R. West (Saskatchewan Health). The author also expresses gratitude to W. M. Samuel and W. D. Wishart for review of the manuscript. The project was supported under contract to Alberta Agriculture.

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Received for publication 8 September 1987.